



Durham E-Theses

Ground beetles and upland plantations

Younes, Miriam

How to cite:

Younes, Miriam (1989) *Ground beetles and upland plantations*, Durham theses, Durham University.
Available at Durham E-Theses Online: <http://etheses.dur.ac.uk/6538/>

Use policy

The full-text may be used and/or reproduced, and given to third parties in any format or medium, without prior permission or charge, for personal research or study, educational, or not-for-profit purposes provided that:

- a full bibliographic reference is made to the original source
- a [link](#) is made to the metadata record in Durham E-Theses
- the full-text is not changed in any way

The full-text must not be sold in any format or medium without the formal permission of the copyright holders.

Please consult the [full Durham E-Theses policy](#) for further details.

GROUND BEETLES AND

UPLAND PLANTATIONS

A case study from Kielder Forest

The copyright of this thesis rests with the author.
No quotation from it should be published without
his prior written consent and information derived
from it should be acknowledged.

Written by Miriam Younes as part of the requirements for the degree of M.Sc in
Ecology at the University of Durham

1989



23 SEP 1992

ACKNOWLEDGEMENTS

I am especially indebted to Dr John Coulson for his supervision and assistance throughout this project. Also to Dr D. Baines for his help, encouragement and ruthless constructive criticisms.

I am also indebted to Dr M. Ireland and Dr J.L. Butterfield for their help in the initial analysis of this work.

Thanks go also to my friends and colleagues at Wytham, especially Ruth Feber for the proof reading of the text and the extra large "halves" of beer provided at last orders in the White Hart. Also to Dr H. Smith for the never ending encouragement when things seemed lost, to Alan Bowman, Dr John Bassett, and Philip Smith, for allowing me the use of their computer equipment and all the other staff at the laboratory for keeping me laughing after late night writing sessions.

CONTENTS

| | |
|--|-----|
| INTRODUCTION..... | P1 |
| CHAPTER 1: BACKGROUND, SITES AND METHODS OF THE STUDY..... | P4 |
| CHAPTER 2: CLASSIFICATION OF SITES USING CARABIDAE..... | P13 |
| CHAPTER 3: THE CARABID COMMUNITIES OF KIELDER..... | P30 |
| CHAPTER 4: THE EFFECTS OF AFFORESTATION ON CARABIDAE..... | P40 |
| CHAPTER 5: CARABIDS AS INDICATORS OF INVERTEBRATES..... | P50 |
| DISCUSSION..... | P68 |
| APPENDICES | |
| REFERENCES | |

INTRODUCTION

British upland plantation forests are a recent phenomenon. At the turn of the century there were only negligible upland planted forests but by 1984 it was estimated that there were one million, three hundred thousand hectares of conifer forest in upland areas of Britain (Forestry Commission 1984). They were the result of a government policy of forest expansion intended to ensure that, if necessary, Britain could be self sufficient in timber for up to 3 years. This idea was first set forward in the 1917 Ackland Committee (Rowan 1985). Given the topography of Britain, it was inevitable that most forest expansion would occur in the uplands.

Many technical problems have had to be overcome to allow this expansion onto wet, exposed uplands. Despite all the achievements, some people view upland afforestation primarily as a disaster to nature conservation. This is because conifer forests are thought to provide poor habitat for wildlife. However, considering its extent, it is probably the least well known habitat for wildlife in the country. Recent publicity of the threats to wildlife from afforestation in the flow country of Caithness and Sutherland has highlighted the need for greater research into nature conservation in upland conifer forests and the Institute of Terrestrial Ecology (I.T.E.) have set up a project to this end. This is based in Kielder Forest in the north of England. Although the main emphasis has been to allow the recognition of plant communities in the forest and their conservation requirements, additional, complimentary invertebrate sampling was also undertaken. This study is a survey of the ground beetles (Coleoptera: Carabidae) of Kielder which constituted a major element of the invertebrate fauna sampled by the I.T.E.



The main questions addressed by this study are:

1) Can distinct communities of carabids be recognised in Kielder and what are the effects of afforestation on any such communities?

2) How reliable are carabids as indicators of general invertebrate communities?

A community is defined as an association of species which recur in a number of sites. These can be recognised using classification techniques which create clusters or classes of sites according to the similarities of their species composition. Chapter 2 compares the results of the classification of the Kielder carabids by two methods: CLUSTAN and TWINSpan. This is complimented by DECORANA which ordines the sites by the carabid composition. Here it is used as a framework in which to compare species and sites with environmental factors in order to help understand the classification results.

Chapter 3 reviews the most meaningful classification of sites by carabids. The species which form the communities of carabids are assessed as to their value as indicator species. An indicator species is defined as being characteristic of the habitat of the relevant community. It should be possible to identify the particular community from the presence of indicator species thus making future surveys easier to carry out.

Chapter 4 investigates the effects of afforestation on the carabid fauna and considers what type of species are most affected by the new environment. This chapter also considers the resilience of the carabid communities to forestry, and investigates whether the original communities will reappear in the event of removal

of the forest cover.

Chapter 5 questions the use of carabids as a key family with which to assess the occurrence of general invertebrate communities. Provided they prove reliable indicators, carabids could, in future, be used as a tool to obtain a relatively easy assessment of invertebrate communities and the effects of environmental changes on them.

CHAPTER 1.

BACKGROUND, SITES AND METHODS OF THE STUDY

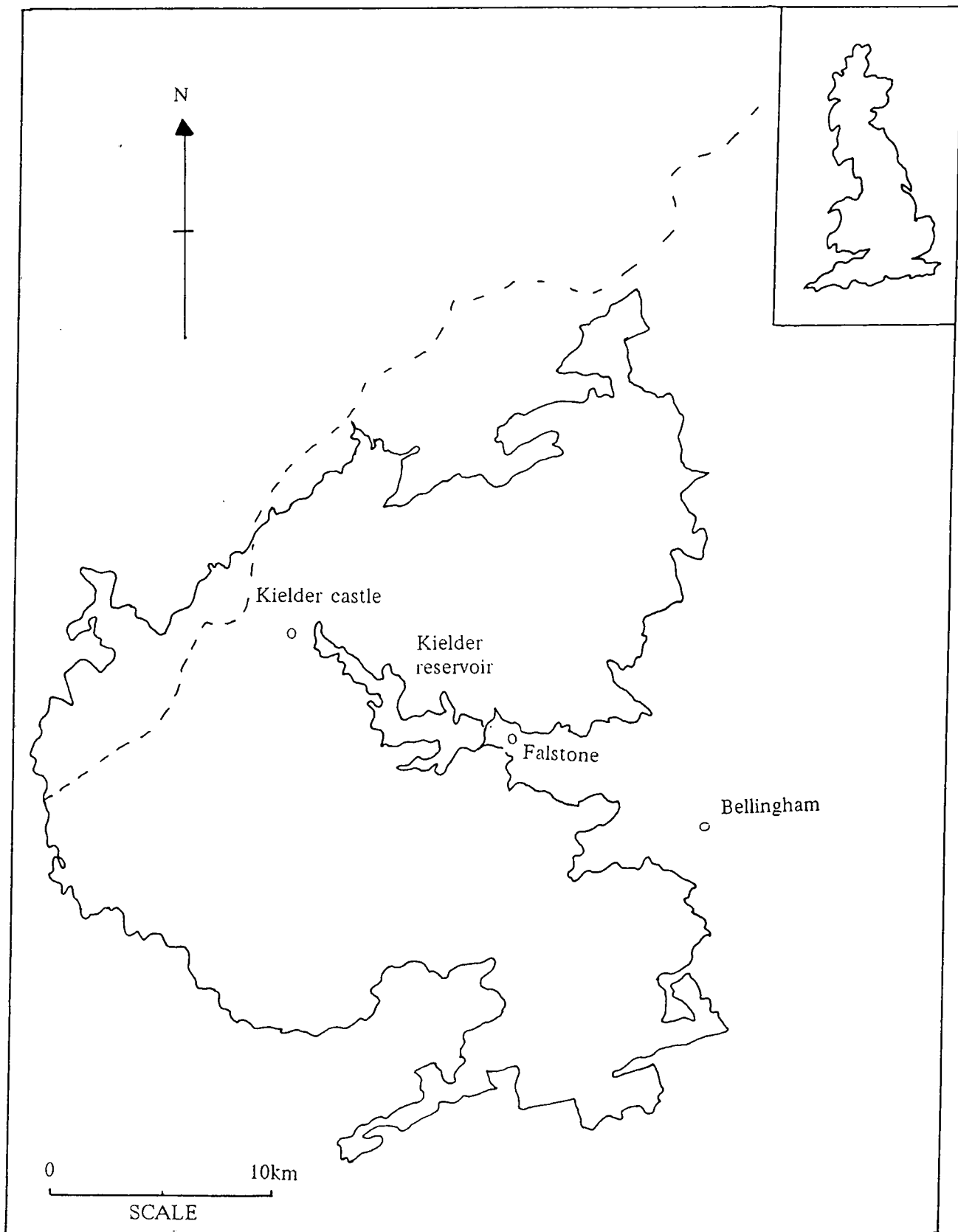
Kielder forest is the largest man made upland plantation in Britain. It has a large range of habitat types with much replication and is therefore ideal as the basis of such a study.

The forest straddles the border between England and Scotland, (figure 1) and covers an area of approximately 600 square Kilometres. The Forestry Commission acquired the land in 1926 and started planting on what was predominantly an extensively farmed sheep grazing area vegetated by *Calluna* and *Molinia* heath.

Deep peat covers about 30% of the area, mostly at high altitudes where rainfall is greatest and temperatures are lowest. A further 50% of the area is covered by boulder clay derived soils which include stagnopodzols, peaty gleys and non peaty gleys. The remainder of the area is covered by mineral soils: brown podzols, brown earths and sandy soils. Sometimes these have a small layer of peat at the surface (peaty skeletal soils and mineral skeletal soils).

The forest crop is predominantly Sitka Spruce (*Picea sitchensis*) which covers about 70% of the total area. Norway Spruce (*Picea Abies*) occupies 15% of the area, chiefly at lower altitudes. Scots Pine (*Pinus sylvestris*) accounts for 3% of the forest although it is too wet for this species and it is no longer planted. Japanese larch (*Larix leptolepis*) covers only 1% of the area and other crops such as Lodgepole Pine (*Pinus contorta*) and broadleaf species are of negligible distribution.

Figure 1a. Map of Kielder Forest area. England/Scotland border is shown by a dashed line.



The average forest rotation lasts approximately fifty years after which time the fully matured trees are clearfelled and a new crop planted.

The preliminary I.T.E vegetation study attempted to classify the major types of vegetation within the forest to allow easy identification in the field. The classification was based on several broad categories of habitats (plantation blocks, rides, restock areas, roads and unplanted areas). The vegetation within each category was classified using two way indicator species analysis (TWINSPAN). The resulting classes were used as the basis of the invertebrate study. A set of 5 pitfall traps were placed in a representative site of each class of vegetation.

The sites with their assigned numbers and individual characteristics are given in table 1. There are three sites in the rides between Sitka Spruce blocks (1,3, and 5) and these are paired with adjacent sites inside the blocks (2,4 and 6 respectively). Site 20 is in a thinned Norway Spruce block. Two sites are on river banks (7 and 14), site 14 is paired with an adjacent site inside the forest block (site 8). Two sites are on road verges (9 and 11), site 9 is paired with adjacent site 10 in a larch block. There are four unplanted sites (15,16,17, and 18). Site 18 is in alder (*Alnus glutinosa*) woodland. Site 19 is in a clearfell area and three sites (12,13 and 14) are in young restocks. In site 12 the Sitka Spruce has reached canopy closure (pole stage), site 13 is in a pre-canopy closure block (thicket stage) and site 14 is in a newly planted larch block.

SAMPLING METHODS

The invertebrates were sampled by 2 methods:

- 1) pitfall trapping,

Table 1 . Physical and vegetation characteristics of the 21 sites sampled in Kielder Forest in 1988. For key see footnote.

| Site | Code | Soil Features: | | | Alt. (m) | Crop Cover | Ground Vegetation: | | |
|------|------|----------------|------|-----|-------------|---------------|--------------------|---------|------|
| | | Group | Type | pH | | | Height | Density | Type |
| 1 | B | P | 1 | 3.5 | 365 | N | 2 | 2 | C |
| 2 | F.S | P | 1 | 3.5 | 365 | C | 0 | 0 | A |
| 3 | B | P | 1 | 3.7 | 320 | N | 2 | 2 | M |
| 4 | F.S | P | 1 | 3.7 | 320 | C | 0 | 0 | A |
| 5 | B | B | 5 | 5.2 | 300 | N | 2 | 2 | MD |
| 6 | F.S | B | 5 | 5.2 | 300 | C | 0 | 0 | A |
| 7 | C | M | 3 | 4.3 | 340 | N | 3 | 2 | J |
| 8 | F.S | M | 3 | 4.3 | 340 | C | 0 | 0 | A |
| 9 | A | MP | 2 | 6.4 | 210 | O | 2 | 2 | D |
| 10 | F.L | MP | 2 | 6.4 | 210 | C | 0 | 0 | A |
| 11 | A | B | 6 | 4.1 | 230 | N | 2 | 2 | M |
| 12 | E.S | B | 4 | 4.0 | 280 | C | 0 | 0 | A |
| 13 | E.S | B | 5 | 3.7 | 220 | O | 1 | 1 | M |
| 14 | E.L | B | 4 | 4.1 | 300 | O | 2 | 2 | D |
| 15 | D | P | 1 | 3.5 | 450 | N | 2 | 2 | C |
| 16 | D | B | 5 | 3.9 | 360 | N | 1 | 1 | M |
| 17 | D | M | 7 | 5.1 | 200 | N | 3 | 2 | DJ |
| 18 | D | M | 8 | 5.1 | 200 | N | 3 | 2 | DJ |
| 19 | D.CF | B | 4 | 4.1 | 225 | N | 1 | 1 | DJ |
| 20 | F.NS | M | 8 | 4.6 | 225 | O | 0 | 0 | A |
| 21 | C | M | 8 | 5.8 | 250 | N | 1 | 2 | DJ |

Footnote

Codes : B = forest ride, A = road, E = restock,
D = unplanted, C = river, CF = clearfell,
F = block, S = sitka, L = larch,
NS = norway spruce.

Soil Group : P = peat, B = boulder clay derived,
M = mineral, MP = mineral with peat overlain.

Soil Type : 1 = deep peat, 2 = peaty skeletal, 3 = sandy,
4 = stagnapodzol, 5 = peaty gley, 6 = non-peaty gley,
7 = brown podzolic, 8 = brown earth.

Crop Cover : C = closed canopy stand, O = open canopy or thinned,
N = no canopy or deciduous,

Veg'n : Height 0 = vegetation zero, 1 = < 0.3 metres,
2 = 0.3 - 1.0 metre, 3 = > 1.0 metre.

Veg'n : Density 0 = vegetation zero, 1 = < 25% cover,
2 = 25 - 75% cover, 3 = > 75% cover.

Veg'n Type : A = vegetation absent,
C = Calluna, Eriophorum, Sphagnum. Wet Peat.
M = Molinia, Deschampsia flexuosa, Calluna. Dry Peat
D = Deschampsia cespitosa, Holcus lanatus, H.mollis
J = Juncus effusus

2) Extraction from soil samples using Berlese-Tullgren extraction funnels.

1) PITFALL TRAPPING

Five pitfall traps were set at each site at 2 metre intervals along a transect. Each trap consisted of a plastic cup (75mm diameter, 110mm deep) placed in the ground with the rim at a level with the surface. They each contained 10 ml of 2% aqueous formalin solution, as a killing agent, and a drop of surfactant detergent to sink the catch.

The traps were in the field from April until October. The contents were collected every 2 weeks or every month at the beginning and end of the sampling period. The invertebrates caught were assigned to different taxonomic groups and the Carabidae identified to species level. The fauna from each of the 5 pitfall traps were summed to produce a total for each site. The numbers of each invertebrate group and each species of carabid caught in the 5 pitfall traps at each site are given Appendices 1 and 2.

Pitfall traps were used because they have several advantages over other methods. They provide a quick and easy means of continuously sampling large numbers of moving invertebrates. This includes nocturnal as well as diurnal species. However, pitfall traps have been widely criticised for use in population studies because catch size is influenced by a wide range of factors other than population size alone. These factors have been reviewed thoroughly by Southwood (1978) and Halsall and Wratten (1988).

The main problem with pitfall traps is that the catches are biased towards certain taxonomic groups or species, particularly the active, highly mobile groups. Consequently the more inactive species will be underrepresented. Greenslade (1961)

suggests that faster moving carabids such as *Pterostichus spp.* are more likely to be captured than the relatively slow moving *Agonum spp.* The method is also biased towards catching ground living fauna so that groups and species which live primarily on the vegetation (e.g. the Hemiptera, and *Demetrias spp.*), or in the soil (e.g. Lumbricidae) are likely to be underestimated. Other biases occur because of the physical characteristics of individual species. For instance, *Notiophilous spp.* are thought to be able to avoid the traps because of their well developed eyesight.

Apart from the biases of pitfall traps towards the capture of certain groups or species, capture is also influenced by the nature of the surrounding vegetation. Ground insects moving through short grass may be able to move faster and therefore be more prone to capture than if moving through long, dense vegetation. This is particularly a problem when comparing catches at different sites with different vegetation composition and structure. In view of the biases, it must be remembered that the spatial distribution of species and groups obtained from pitfall traps will not necessarily reflect those of the populations under study. However, several people, including Baars (1979) and Cory (1984) have shown that for the carabids, pitfall trap catches made throughout the year allow an adequate estimation of population densities.

2)EXTRACTION FROM SOIL SAMPLES

This method was used to provide information on less mobile species of invertebrates that are seldom caught in pitfall traps. In April and September, 5 replicate soil samples of 30cm square and 10cm deep were collected from each site close to the pitfall traps. The soil fauna were extracted from these samples using a Berlese-Tullgren extraction funnel (Southwood 1978). This is a behavioural method of extraction whereby the animals leave the substrate under a heat stimulus from a light

source. The efficiency of this method varies according to soil types and animal groups. Some groups, such as Coleoptera larvae for instance, are prone to desiccation. Despite this, it can give a good relative indication of the densities of soil invertebrates in the top layers of the soil.

The fauna collected from Kielder were sorted into major groups and their densities estimated. The results are given in Appendix 3.

METHODS OF CLASSIFICATION AND ORDINATION

Two methods of classification, CLUSTAN and TWINSpan were used for the carabid data to find groups of sites which have distinct carabid communities. The ordination method DECORANA was used to find the most important environmental gradients affecting the carabids.

CLUSTAN

This is an agglomerative hierarchical multivariate method of classification which is based on a matrix of similarities of the fauna within the sites. The index of similarity used here is the Czekanowski–Dice coefficient

The CLUSTAN package uses binary data allowing some weight to be given to the most abundant species or taxa. "Pseudospecies" have been created above certain levels of abundance. With respect to carabids, any site in which more than 29 individuals of one species have been caught is considered to have 2 pseudospecies. If between 1 and 29 individuals have been caught this site is assumed to have only 1 pseudospecies. The value of 29 has been chosen to allow 30% of all species to count as 2 pseudospecies. The corresponding cut off values for the soil invertebrate groups are

49, 99 and 999 individuals per 5 metres squared and for the pitfall trapped invertebrate groups are 14, 149 and 749 individuals.

From the resulting similarity matrix, CLUSTAN constructs a hierarchical classification dendrogram by joining the two most similar sites together to form the basis of a group. The similarity of this group to all other sites is calculated (the level of similarity). The next 2 most similar sites are merged together or, if they are more alike, the first group and another site. Eventually all the groups are merged. The sites were clustered in this study using the Average Linkage Method (Sneath and Sokal 1973)

TWO WAY INDICATOR SPECIES ANALYSIS (TWINSpan)

This is a divisive hierarchical method of classification derived from indicator species analysis (Hill et al. 1975). The method works by ordering the sites according to their fauna, by reciprocal averaging, then calculating site scores based on this ordination. The sites are then divided along the principal variation axis using a mean of the site scores. This is modified by the identification of species which best indicate the opposing sides of the division. The sites are further scored as to the presence or absence of these species and a modified division occurs. The original ordination division is then adjusted to give the best possible compromise between the two divisions. Further divisions occur in the same way for each side of the principal division until all the sites have been separated.

TWINSpan is a modification of indicator species analysis because it classifies both samples and species. This is used to produce an ordered two way table of the original data. As with CLUSTAN, data have been transformed using the same pseudospecies conditions as described above.

DETRENDENED CORRESPONDANCE ANALYSIS (DECORANA)

DECORANA is a multivariate ordination technique. An ordination is a spatial arrangement of samples such that their position reflects their similarity. This is likely to be in response to environmental factors affecting the species composition. This method uses a modified version of reciprocal averaging to order both the sites and the species (Hill 1973) along principal axes. The main axes are displayed in graphical form. This can then be used to search for the causal factors of the variations and therefore can help to explain the classification produced by CLUSTAN and TWINSpan.

OTHER METHODS

A measure of diversity has been used throughout this study which is derived from the percentage of the catch comprised by the five most abundant species at a site. This simple measure takes into account both the number of species and the evenness of abundance of species captured at a site. The lower the value, the more diverse the fauna of a site is considered to be. All the calculations were repeated using a more complicated diversity index known as Williams alpha (Southwood 1978) but the results remained the same. The simple value used here was therefore considered adequate for this study.

CHAPTER 2.

CLASSIFICATION OF SITES USING CARABIDAE

The aim of this chapter is to identify discrete communities of carabids in Kielder using an appropriate classification technique. The results of TWINSpan and CLUSTAN classifications of the sites by the species composition are compared, to determine which is the most biologically meaningful. Additionally, DECORANA is used to aid the interpretation of the classification.

TWO WAY INDICATOR SPECIES ANALYSIS (TWINSpan)

Using TWINSpan on the carabids caught in pitfall traps, the sites classified into three groups. The dendrogram formed from the analysis is shown in figure 2a and summarised in figure 2b.

The species of carabids appear to fall into four groups; those marked with an asterisk are the TWINSpan indicator species.

W - WIDESPREAD SPECIES.

Leistus rufescens (Fabricius), *Patrobus assimilis* (Chaudoir), *P. atrorufus** (Strom),
Cychnus caraboides (Linnaeus), *Pterostichus adstrictus* (Eschscholtz), *Notiophilus biguttatus* (Fab.), *Nebria salina* (Fairmaire), *Carabus problematicus* (Herbst.),
Trechus obtusus (Erichson), *T. secalis* (Paykull) and *T. rubens* (Fab.).

Figure 2a. The Classification of Sites by TWINSpan using the Composition of Carabid Species

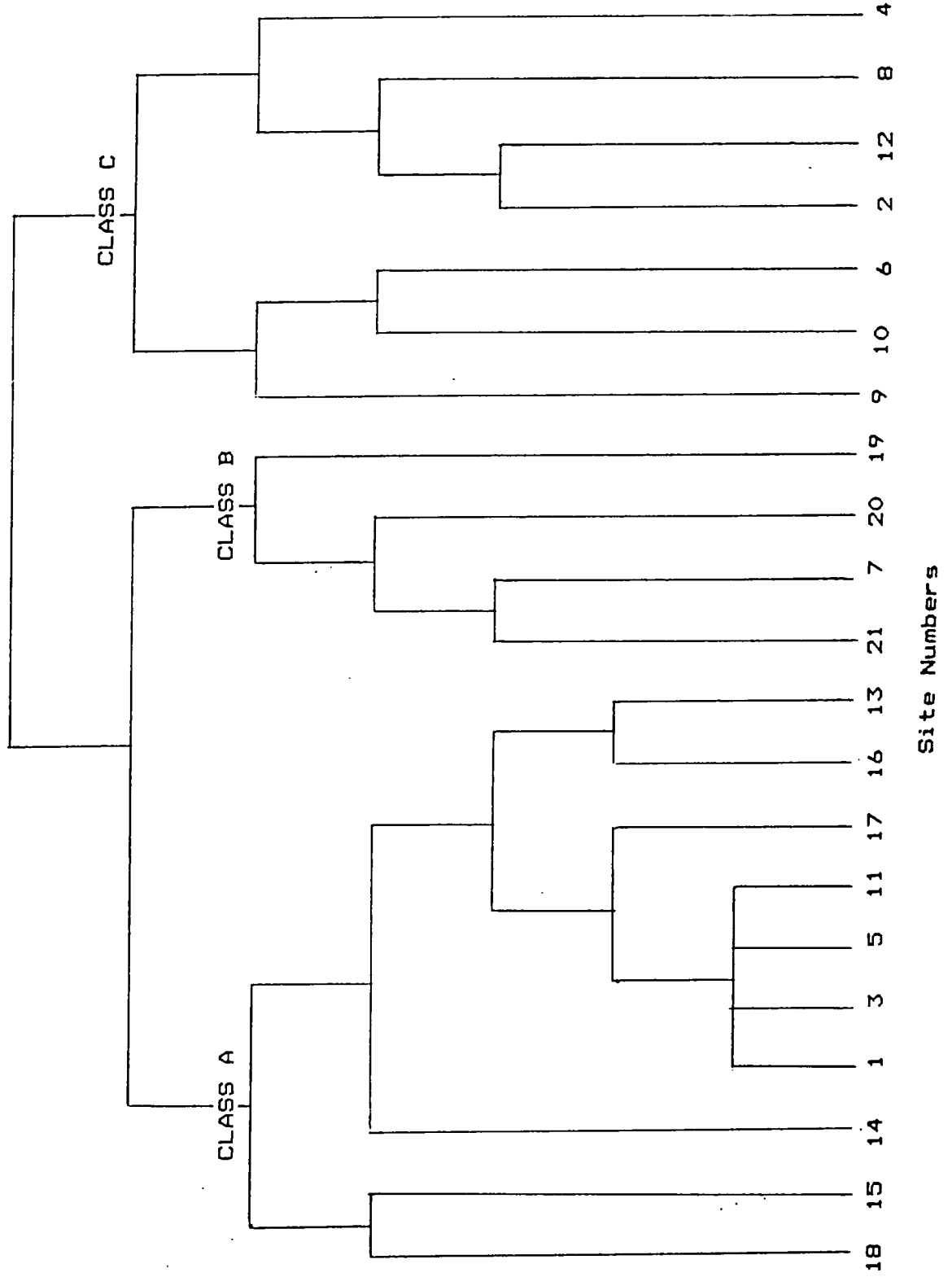
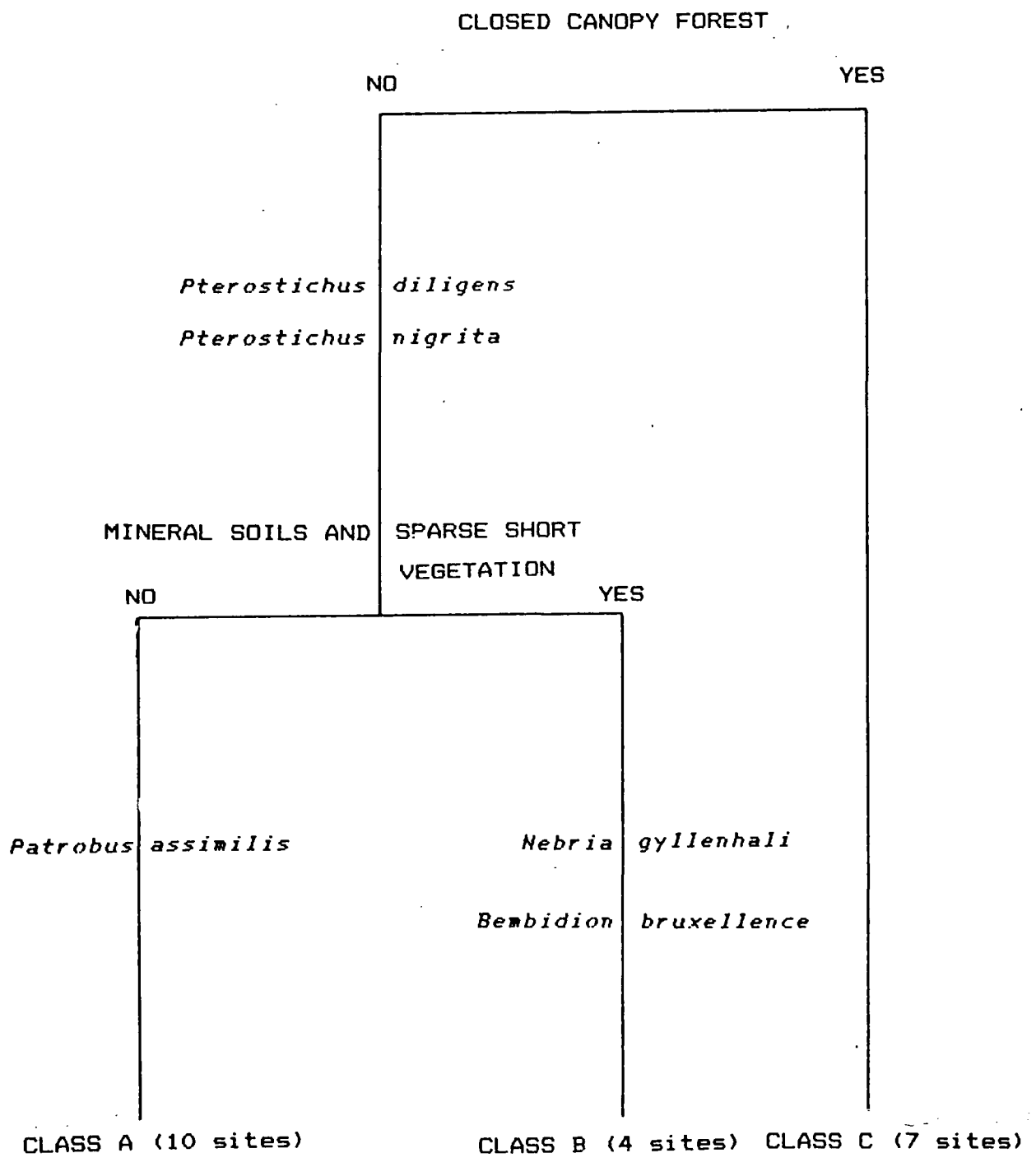


Figure 2b. Summary Dendrogram showing the 3 TWINSpan Classes, with Indicator Species for the Carabidae.



X - NON-FOREST TOLERANT SPECIES.

Notiophilus aquaticus (L.), *N.palustris* (Duft.), *Agonum fuliginosum* (Panzer), *Pterostichus diligens** (Sturm), *P.strenuus* (Pan.), *P.niger** (Schaller), *P.nigrita* (Pay.)(see footnote), *P.madidus* (Fab.), *Amara lunicollis* (Schiodte), *A.communis* (Pan.), *Abax parallelepipedus* (Piller), *Carabus violaceus* (L.) and *Bembidion unicolor* (Chaud.).

Y - SPECIES OF OPEN SITES WITH LUSH VEGETATION MAINLY ON PEATY SOILS.

Carabus glabratus (Pay.), *Notiophilus germinyi* (Fab.), *Dyschirius globosus* (Herbst.), *Amara aulica* (Pan.), *Agonum versutum* (Sturm), *Pterostichus cristatus* (Dufour), *Trichocellus placidus* (Gyllenhal) and *Bradycellus harpalinus* (Sreville).

Z - SPECIES OF OPEN SITES WITH SHORTER VEGETATION ON SANDY SOILS.

Carabus granulatus (L.), *C.nemoralis* (Muller), *Elephrus cupreus* (Duft.), *Clivina fossor* (L.), *Pterostichus melanarius* (Illiger), *P.vernalis* (Pan.), *P.versicolor* (Sturm), *Agonum muelleri* (Herbst.), *A. albipes*, (Fab.), *Nebria gyllenhalii** (Schönherr), *N.brevicollis* (Fab.), *Bembidion bruxellense** (Wesmael), *Loricera pilicornis* (Fab.) and *Calathus micropterus* (Duft.).

The main division by TWINSPAN is between those sites which only contain group W species and those which also have group X species (indicated by *Pterostichus diligens* and *Pterostichus niger*). The sites without group X species form class C of the TWINSPAN dendrogram and are found below a closed canopy of Sitka Spruce and larch. One site (site 12) is a restock but the crop is at the "pole" stage of growth and the canopy has closed. Only site 9 appears anomalous because it lies on a roadside verge

Footnote. The form of the right aedeagal paramere indicates that the species found in Kielder is *Pterostichus nigrita* and not the identical species, *P. rhaeticus* (Heer.)

adjacent to a larch block. Only one species of carabid, *Trechus secalis*, is confined to this class.

The sites with group X species have been further divided into 2 classes depending on whether they also contain group Y or group Z carabids. However, this division is tentative because all the species of group Y are rare, nowhere forming more than 10% of the total catch. Furthermore, the majority of species included in group Z have been caught at only one site (site 21). To test the validity of this division, the more common beetles were extracted from the data in an attempt to find associations of carabid species (Table 2a).

Two associations of carabids can be identified (TS1 and TS2). Association TS1 consists of carabids which, according to Lindroth (1985), are tolerant of open conditions and prefer mineral soils. The 4 sites of class B in which this association appears, all lie on mineral soils except for site 19 which is on boulder clay derived stagnopodzol. Where present, the ground vegetation is sparse and short. Conversely, the carabids which make up association TS2 are mostly hygrophilous and seem to prefer the wet conditions of the peaty or boulder clay soils frequent in class A sites. However, where mineral soils prevail, (eg. sites 18 and 17) the ground vegetation is tall and lush. This may retain moisture better than the sparse vegetation found in class B sites.

The division of classes A and B therefore, may be valid biologically despite the reservations described above. TWINSpan picked out two positive indicator species for class B, *Nebria gyllenhali* and *Bembidion bruxellense*. A negative indicator species, *Patrobus assimilis* has also been identified for this class. It is not found in class B sites despite being found in most other sites including those of class C. This

Table 2a. Associations of carabid species which form 10% or more of the seasonal catch or exceeded 10 individuals in 2 or more sites in each TWINSPAN group.

X = 10 or more individuals caught or forming more than 10% of the catch/site.
 . = present at a site.

| | CLASS A | | | | | | | | | | CLASS B | | | | CLASS C | | | | | | |
|-----------------|---------|----|----|---|---|---|----|----|----|----|---------|---|----|----|---------|----|---|---|----|---|---|
| | 18 | 15 | 14 | 1 | 3 | 5 | 11 | 17 | 16 | 13 | 21 | 7 | 20 | 19 | 9 | 10 | 6 | 2 | 12 | 8 | 4 |
| T.obtusus | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| C.problematicus | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| P.madidus | X | X | . | . | . | . | X | X | X | . | . | . | X | X | X | . | X | . | . | X | X |
| C.violaceus | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| N.brevicollis | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| L.pilicornis | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| P.diligens | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| P.niger | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| P.nigrita | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| A.fuliginosum | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| A.lunicollis | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| P.assimilis | X | X | X | X | X | X | . | . | . | . | . | . | . | . | . | . | X | X | X | X | X |

ASSOCIATIONS
 T52
 T51

carabid is described by Lindroth (1985) as hygrophilous and is therefore absent from the drier mineral soil sites.

CLUSTAN ANALYSIS

CLUSTAN has an advantage over TWINSpan in that it produces a quantifiable dendrogram. The degree of similarity of sites within a cluster can be assessed from the vertical axis of this dendrogram. Figure 2c was produced from the Kielder carabid data. It is not obvious at what level of similarity the clusters should be separated, but level 0.39 was chosen because it is of a high enough similarity to make the clusters meaningful, yet low enough to produce the separation of the two major non-forested clusters A and B. When common beetles were extracted and associations sought, (Table 2b) separate associations could be identified within these clusters so the level of similarity used appears to be valid.

CLUSTAN separates the closed canopy Sitka Spruce and larch blocks from all other sites at a similarity of less than 0.25. This shows that these plantation sites are very unlike other areas of the forest with respect to their carabid fauna. Three clusters of low similarity have been formed in this instance. Cluster C is made up of sites 2, 12 and 6 which all support very low numbers of carabids, 12, 6 and 4 individuals respectively, with *Patrobus assimilis* the most frequently caught species. Sites 4 and 8 form cluster D and are similarly impoverished with *Trechus obtusus* dominant numerically. Sites 9 and 10 have been grouped together as cluster E and have more carabid species and individuals than the other plantation sites. These sites are typified by large numbers of *Trechus secalis*. None of these plantation sites support any strong associations of carabids (Table 2b) and with the exception of sites 9 and 10 have very low numbers of individuals. Consequently, they are considered as a

Figure 2c. The Classification of Sites by CLUSTAN using the Composition of Carabid Species

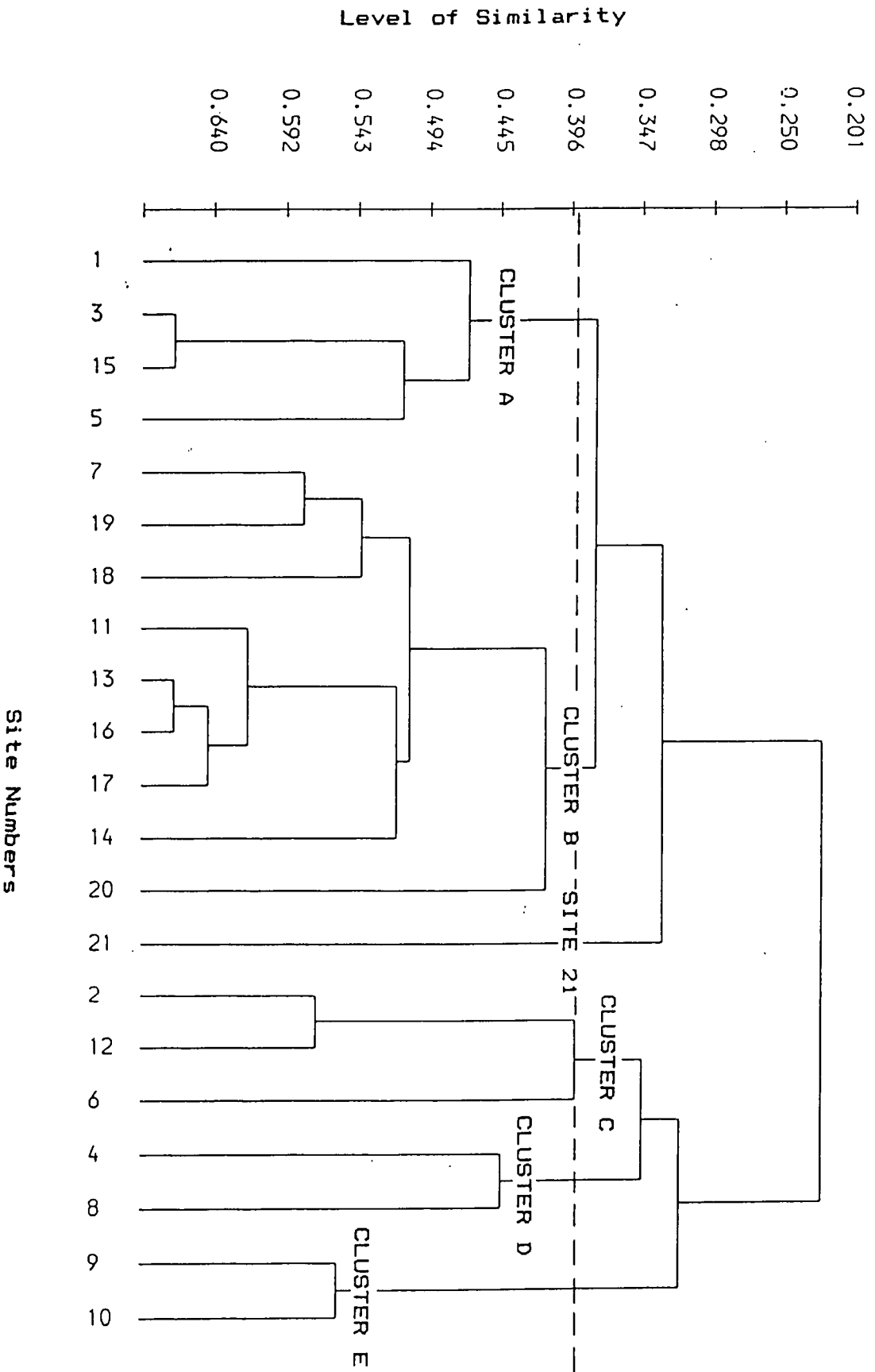


Table 2b. Associations of carabid species which form 10% or more of the seasonal catch or exceeded 10 individuals in an at least 2 of the CLUSTAN groups.

X = 10 or more individuals or forming more than 10% of the catch / site.

. = present at a site.

| ASSOCIATION | CLUSTER A | | | | | CLUSTER B | | | | | | | CLUSTERS C,D,E | | | | | | | | |
|--------------|-----------|---|----|---|---|-----------|----|----|----|----|----|----|----------------|----|---|----|---|---|---|---|----|
| | 1 | 3 | 15 | 5 | 7 | 19 | 18 | 11 | 13 | 16 | 17 | 14 | 20 | 21 | 2 | 12 | 6 | 4 | 8 | 9 | 10 |
| C1 | X | X | X | X | X | | | | | | | X | X | X | X | X | X | X | X | | |
| P. assimilis | | | | | | | | | | | | | | | | | | | | | |
| P. nigrita | X | X | X | X | X | | | | | | | X | X | X | | | | | | | |
| P. diligens | X | X | X | X | X | | | X | X | | | | | | | | | | | | |

| ASSOCIATION | CLUSTER A | | | | | CLUSTER B | | | | | | | CLUSTERS C,D,E | | | | | | | | |
|------------------|-----------|---|----|---|---|-----------|----|----|----|----|----|----|----------------|----|---|----|---|---|---|---|----|
| | 1 | 3 | 15 | 5 | 7 | 19 | 18 | 11 | 13 | 16 | 17 | 14 | 20 | 21 | 2 | 12 | 6 | 4 | 8 | 9 | 10 |
| C2 | X | X | X | X | X | | | | | | | X | X | X | X | X | X | X | X | | |
| C. violaceus | | | | | | | | | | | | | | | | | | | | | |
| C. problematicus | | | | | | | | | | | | | | | | | | | | | |
| L. rufescens | | | | | | | | | | | | | | | | | | | | | |
| N. biguttatus | | | | | | | | | | | | | | | | | | | | | |
| L. pilicornis | | | | | | | | | | | | | | | | | | | | | |
| P. madidus | | | | | | | | | | | | | | | | | | | | | |
| P. niger | | | | | | | | | | | | | | | | | | | | | |
| C. micropterus | | | | | | | | | | | | | | | | | | | | | |
| A. fuliginosum | | | | | | | | | | | | | | | | | | | | | |
| A. lunicollis | | | | | | | | | | | | | | | | | | | | | |

single group.

At the 0.39 level of similarity, CLUSTAN produced 2 more clusters and identified a single site (site 21) as being dissimilar to the rest. Table 2b shows that different associations of carabids correspond to these separate clusters ie. association C1 corresponds to cluster A whereas association C2 corresponds to cluster B. Cluster A sites are primarily situated on deep peat soils, whereas cluster B sites are on shallow peat or mineral soils.

Site 21 differs from other non-forested sites by containing large numbers of carabids unique to this site, for example, *Agonum muelleri*, *Pterostichus versicolor* and *Pterostichus vernalis*. In addition, rarer species such as *Elephras cupreus*, *Carabus granulatus* and *C. nemoralis* are only found here.

DECORANA ANALYSIS

Both CLUSTAN and TWINSpan classifications have separated the closed canopy Sitka Spruce and larch sites from the rest suggesting that the presence of tree cover is the most important influence on the carabid communities of Kielder. This is supported by DECORANA with the main axis of both the site scores (Figure 2d) and the species scores (Figure 2e) being related to tree cover. The sites on the right hand side of axis 1 in figure 2d lie under closed canopy Sitka Spruce or larch blocks. Those in the middle tend to be under canopies of broadleaved species or Norway Spruce and those towards the left of the axis are open rides, unplanted and restock sites. Similarly, axis 1 of figure 2g, suggests there is a continuum of carabids with those that were present below a closed canopy (e.g. *Trechus secalis*) occurring towards the extreme right of the axis, whereas those not present in this environment (eg.

Figure 2d Plot of Site Scores Axis 1 and 2 Identified by DECORANA for Carabid Species

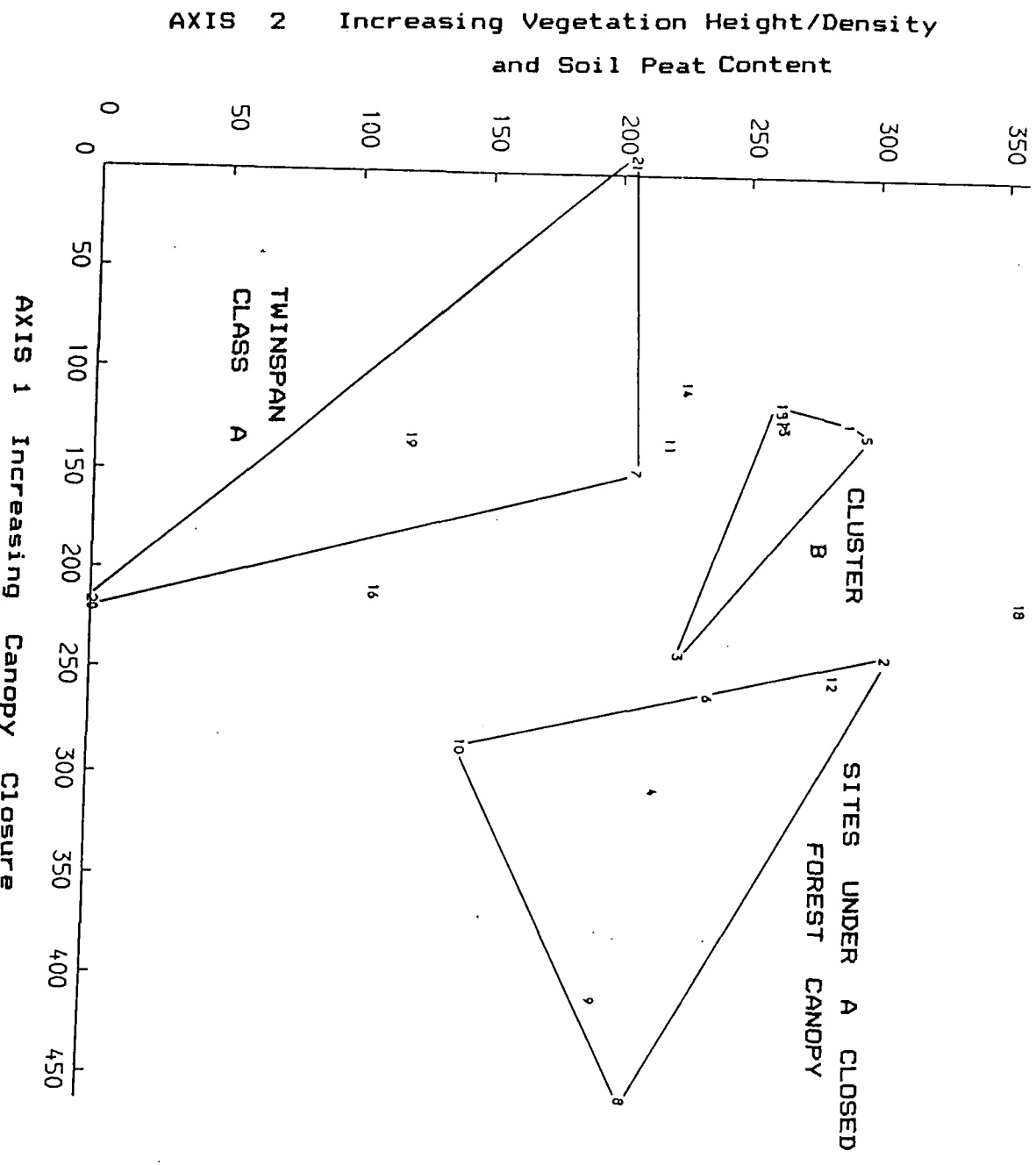
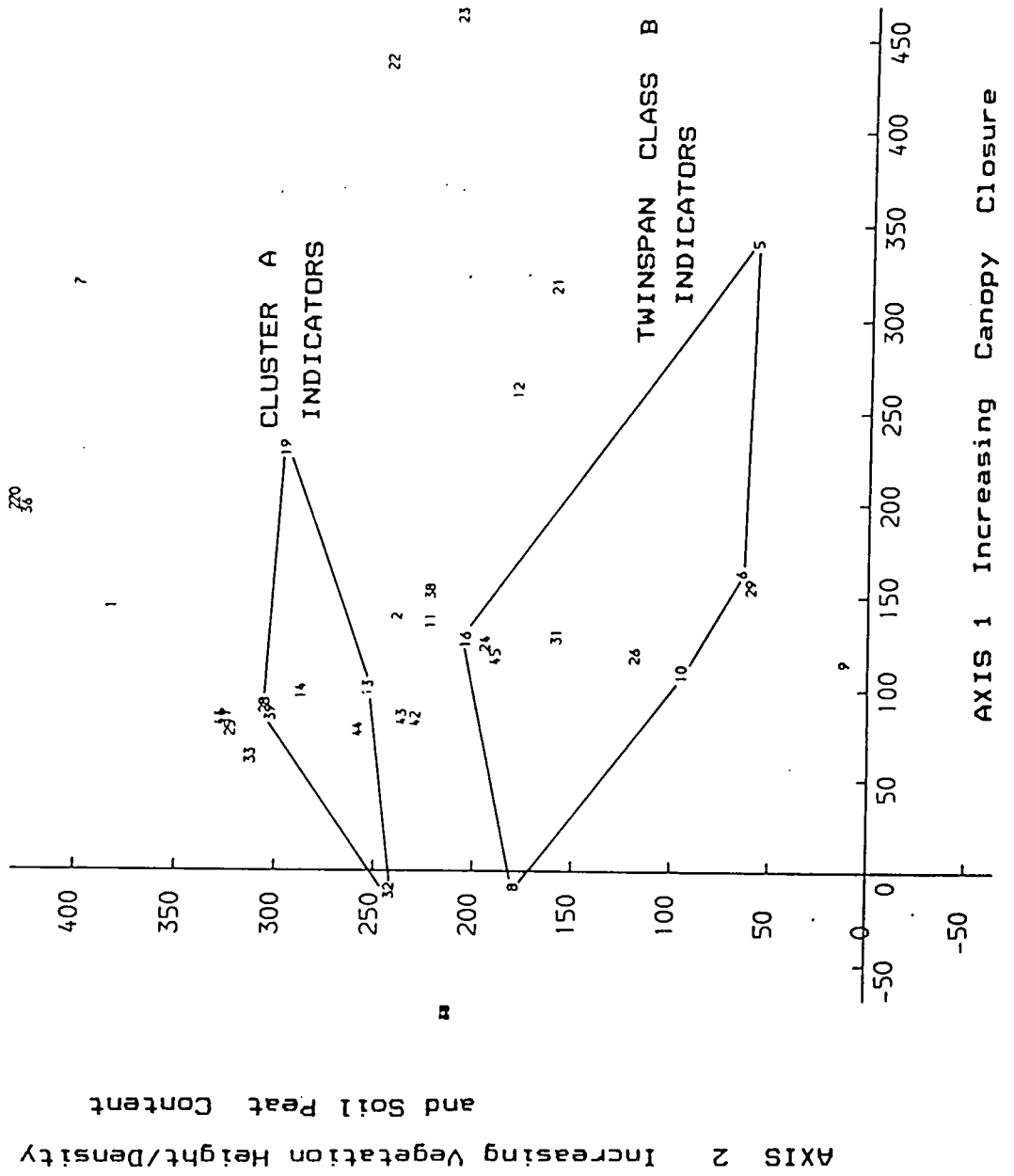


Figure 2e. Plot of Species Scores Axis 1 and 2 Identified by DECORANA for Carabid Species



Pterostichus niger) lie to the extreme left.

It is not clear which classification is most appropriate for sites not under a closed forest canopy. TWINSPAN has separated the sites on mineral soils with sparse vegetation from the rest, whilst CLUSTAN has separated off those with deep peat soils. DECORANA suggests there is some sort of separation along axis 2 of both species and sites, relating to these two extremes. Figure 2d shows that the association of carabids formed on deep peat soils, identified by CLUSTAN as cluster A, (*Pterostichus diligens*, *Patrobus atrofusus* and *Pterostichus nigrita*) occur in the upper part of axis 2. Conversely, those species forming an association on mineral soils with low vegetation distinguished by TWINSPAN as class B (*Carabus problematicus*, *Carabus violaceus*, *Nebria brevicollis* and *Loricera pilicornis*) lie towards the bottom of this axis. Furthermore, the peat sites of cluster A (1,3,5 and 15) lie towards the top of axis 2 in figure 2e whereas the mineral sites of TWINSPAN class B (7,19,20 and 21) lie towards the bottom of the axis.

However, sites not relating to these extreme groups (11,13,14,16,17 and 18) cause confusion with the classification and ordination. This could be a symptom of attempting to impose a classification on essentially continuous data. It is likely that a continuum of conditions occurs in the unforested areas of Kielder ranging from deep peat soil areas to those with mineral soils and short vegetation. Two different classifications have isolated the opposite extremes of the continuum and it remains unclear which classification has produced the most biologically meaningful results. It is therefore necessary to consider this further from another point of view.

WHICH CLASSIFICATION IS THE MOST MEANINGFUL?

When associations of beetles were sought for each classification as shown by Tables 2a and 2b, both techniques appear to have produced biologically meaningful results as far as species preferences are concerned. If these associations are truly valid, they may form the basis of different communities with different structural characteristics. These are now investigated in order to verify the classification techniques.

Table 2c presents three measures of carabid community structure:

i) the number of individuals caught at each site,

ii) the number of species caught,

iii) the percentage of the total catch accounted for by the 5 most abundant species at each site.

The means \pm 1 standard error of these measures were calculated for each association depicted by both CLUSTAN and TWINSpan as shown in tables 2d and 2e. Student's t-tests were applied to investigate whether these characteristics of the structure of community were significantly different between the associations formed by the two classifications.

No significant differences were found between associations T1 and T2 of TWINSpan and consequently, these associations are unlikely to form separate communities. However, the CLUSTAN associations were more robust. There were significant differences for all

Table 2c. Measurements of carabid community structure for each of the 21 sites sampled in Kielder Forest in 1988.

| Site No. | No.Individuals | No.Species | % top five spp. to total |
|----------|----------------|------------|-----------------------------|
| ----- | | | |
| 1 | 57 | 8 | 95 |
| 2 | 12 | 2 | 100 |
| 3 | 34 | 7 | 94 |
| 4 | 25 | 5 | 100 |
| 5 | 64 | 8 | 92 |
| 6 | 4 | 2 | 100 |
| 7 | 52 | 15 | 77 |
| 8 | 9 | 3 | 100 |
| 9 | 310 | 10 | 98 |
| 10 | 106 | 8 | 96 |
| 11 | 122 | 19 | 56 |
| 12 | 6 | 5 | 100 |
| 13 | 194 | 18 | 79 |
| 14 | 170 | 14 | 76 |
| 15 | 25 | 8 | 84 |
| 16 | 193 | 18 | 82 |
| 17 | 121 | 23 | 64 |
| 18 | 222 | 16 | 84 |
| 19 | 590 | 17 | 94 |
| 20 | 636 | 12 | 97 |
| 21 | 600 | 24 | 84 |

Table 2d. The mean number (\pm 1S.E.) of individual carabids, number of species caught and the percentage of individuals in each TWINSPAN class comprised by the five most numerous species.

| | Individuals | : | Species | : | % top five spp to total |
|-----------------------|--------------|---|----------------|---|----------------------------|
| Class A (10 sites) | 120 \pm 23 | : | 13.9 \pm 1.8 | : | 81 \pm 4 |
| Class B (4 sites) | 470 \pm 93 | : | 17.0 \pm 2.3 | : | 88 \pm 5 |
| Class C (7 sites) | 67 \pm 43 | : | 5.0 \pm 1.2 | : | 99 \pm 6 |

Table 2e. The mean number (\pm 1S.E.) of individual carabids, number of species caught and the percentage of individuals in each CLUSTAN cluster comprised by the five most numerous species.

| | Individuals | : | Species | : | % top five spp. to total |
|------------------------------|--------------|---|----------------|---|-----------------------------|
| Cluster A (4 sites) | 45 \pm 9 | : | 7.7 \pm 0.3 | : | 91 \pm 3 |
| Cluster B (9 sites) | 256 \pm 70 | : | 16.9 \pm 1.6 | : | 79 \pm 4 |
| Clusters C,D,E. (7 sites) | 67 \pm 43 | : | 5.0 \pm 1.2 | : | 99 \pm 1 |

three measures of community structure between CLUSTAN associations C1 and C2. Cluster B sites had significantly more individuals than those in Cluster A ($t=2.99$ $df=9$ $P<0.05$). The number of species was also greater in cluster B ($t=8.39$ $df=9$ $P<0.01$) and the percentage that the top 5 species contribute to total numbers was significantly less in cluster B than A ($t=2.45$ $df=9$ $P<0.05$). Therefore the CLUSTAN associations of sites not under a closed forest canopy are distinct as far as community structure is concerned and can be considered to be different communities, C1 and C2.

There were also significant differences in community structure measurements between community C2 and the closed canopy Sitka Spruce and larch sites. The number of individuals was found to be greater in community C2 sites ($t=2.35$ $df=11$ $P<0.05$). The number of species was also greater ($t=7.58$ $df=13$ $P<0.01$) and the percentage of the catch accounted for by the top 5 species was less in community C2 ($t=4.66$ $df=8$ $P<0.01$). The forested sites are more impoverished and less diverse than community C2 sites. However, when the forested sites were compared to community C1 no significant differences were found.

CONCLUSION

CLUSTAN carabid communities have been found to be distinct entities with respect to community structure variations. Hence, CLUSTAN is the classification technique most appropriate to this study. It should be possible to identify communities from the species which reccur within them. Consequently, the species comprising communities C1 and C2 can be thought of as indicator species. Cluster B sites have a more diverse community than cluster A sites and contain the indicator species of association C2, whereas Cluster A sites contain the indicator species of association C1. CLUSTAN has also identified a site which is separated from all others on the basis of its carabid fauna, Site 21. The following chapter thoroughly reviews the classification results.

CHAPTER 3.

THE CARABID COMMUNITIES OF KIELDER

Now that the most meaningful classification has been chosen, the habitats of the sites which make up each cluster can be considered along with the associated community of carabids, where they have been identified. The reliability of the indicator species of communities C1 and C2 are considered. A species is considered a reliable indicator if it fulfills one or more of three criteria:

- i) it has been caught in a high frequency of sites within the cluster,
- ii) it has been caught in greater numbers than in other clusters,
- iii) it is exclusive to the cluster.

It should also be indicating habitats consistent with those identified by other studies.

For ease of interpretation, all sites that are not under closed canopy forest are described as open. This includes deciduous woodland and thinned forest sites.

CLUSTER A - Open sites on deep peat comprising carabid community C1.

The sites which make up this cluster are on plantation rides at relatively high altitudes (359 +/- 33m) or on open moorland (site 15) and are chiefly situated on deep peat acid soils (pH 3.9 +/- 0.4). The vegetation is dense and of medium height.

Sites 1 and 15 are dominated by *Calluna vulgaris* whereas *Molinia caerulea* and *Deschampsia* species dominate on sites 3 and 5.

Site 5 is the least characteristic of the sites within this class because it is on a boulder clay derived peaty gley soil rather than pure peat. However, it has a similar carabid fauna to the other sites within cluster A. Adequate numbers of the indicator species of community C1 were captured, whilst the indicator species identified for cluster B sites were largely absent. The carabid fauna appears typical of a ride in an upland plantation.

Community C1 consists of both fewer species and numbers of individuals than community C2. The indicator species are *Patrobus assimilis*, *Pterostichus nigrita* and *P. diligens*. The mean numbers of these species captured per site within each class is shown in Table 3a along with the indicator species of cluster B and important species of site 21 and clusters C,D and E.

Patrobus assimilis appears to be the most reliable indicator species of community C1. It was caught in all 4 sites and was the only indicator to be caught in greater numbers here than elsewhere. This species appears to prefer areas of deep peat, even if under closed canopy forest. It is absent from only 5 sites, all of which lie on mineral soils. Significantly more specimens of *Patrobus assimilis* were caught on peat than on mineral sites ($t=3.59$, $DF=13$, $P<0.01$). The tendency of this species to form an important component of the carabid communities of peaty upland sites is further substantiated by the findings of Lindroth (1985) and the studies of Butterfield and Coulson (1983) and Luff and Rushton (1989).

Neither *Pterostichus diligens* nor *P. nigrita* are such reliable indicators of community C1 as *Patrobus assimilis* because they are more common on the sites of

Table 3a The mean number of indicator species of communities C1 and C2 and the more important species of the other clusters (+/-1S.E.) per site in each cluster.

| | CLUSTER A | CLUSTER B | SITE 21 | CLUSTERS C,D,E. |
|--------------------------------|--------------|---------------|---------|-----------------|
| <u>Patrobus assimilis</u> | 10.2 +/- 3.0 | 3.0 +/- 1.9 | 0 | 3.4 +/- 1.3 |
| <u>Pterostichus nigrita</u> | 3.7 +/- 1.7 | 6.2 +/- 3.9 | 161 | 0 |
| <u>P.diligens</u> | 16.0 +/- 5.9 | 18.0 +/- 12.1 | 4 | 0 |
| <u>Carabus violaceus</u> | 0.5 +/- 0.3 | 8.9 +/- 3.3 | 0 | 0 |
| <u>Leistus rufescens</u> | 1.0 +/- 0.4 | 6.9 +/- 2.5 | 0 | 5.1 +/- 1.2 |
| <u>Calathus micropterus</u> | 0 | 42.0 +/- 38.9 | 0 | 0.3 +/- 0.3 |
| <u>Amara lunicollis</u> | 0 | 8.3 +/- 5.8 | 0 | 0 |
| <u>Notiophilus biguttatus</u> | 0 | 7.6 +/- 4.1 | 1 | 1.1 +/- 0.5 |
| <u>Carabus problematicus</u> | 0 | 20.4 +/- 9.0 | 9 | 5.1 +/- 4.2 |
| <u>Agonum fuliginosum</u> | 2.5 +/- 2.5 | 3.6 +/- 2.3 | 1 | 0 |
| <u>Loricera pilicornis</u> | 0.3 +/- 0.3 | 5.0 +/- 2.7 | 24 | 0.3 +/- 0.3 |
| <u>Pterostichus niger</u> | 0.3 +/- 0.3 | 8.2 +/- 3.8 | 11 | 0 |
| <u>P.madidus</u> | 1.0 +/- 0.7 | 38.4 +/- 18.9 | 8 | 0.3 +/- 0.3 |
| <u>Trechus obtusus</u> | 4.2 +/- 4.2 | 6.4 +/- 3.4 | 2 | 3.0 +/- 1.8 |
| <u>T.secalis</u> | 0 | 0 | 0 | 47.0 +/- 34.7 |
| <u>Pterostichus versicolor</u> | 0 | 0 | 14 | 0 |
| <u>P.vernalis</u> | 0 | 0 | 14 | 0 |
| <u>Agonum muelleri</u> | 0 | 0 | 104 | 0 |

cluster B. These hygrophilous species may not only be attracted to the high moisture content of the peat soils of cluster A, but also to other wet sites on mineral soils. For example, *Pterostichus nigrita* was caught in large numbers at site 21 which is on mineral soil adjacent to a river and at sites 14 and 17 which support high dense vegetation able to hold moisture. It is absent from 5 sites within cluster B and with one exception, these appear to be drier with only short sparse vegetation. The absence of both these species from mature forest sites is possibly due to soil drainage.

In accordance with these results, Lindroth (1985) described both these species as being confined to moist sites. Butterfield and Coulson (1983) found them to be rare on the drier upland grassland sites and the drier peat sites of uplands in northern England, but part of the associations indicative of the wetter peat sites.

Individually, neither *Pterostichus diligens* nor *P.nigrita* appear to be reliable indicators of peaty moorland sites since they are also common on other open sites. Conversely, *Patrobus assimilis* was largely restricted to peat soils but was captured within the closed canopy forest sites. However, when all three species are found together they indicate open situations on damp peaty soils.

CLUSTER B – Open sites on shallow peat or mineral soils comprising carabid community C2.

These sites are less homogenous than those of cluster A with respect to both the habitat characteristics and the indicator species present. It is possible that a more extensive survey of open sites on shallow peat or mineral soils would reveal more clusters. The dendrogram suggests there may be a division beginning to separate sites 7, 19 and 18 from sites 11, 13, 16, 17 and 14 at similarity level 0.5, but as

this lies above the chosen value it will not be considered.

The average altitude of these sites is 255m (+/-20m) above sea level and the mean soil pH is 4.3 (+/- 0.2). Although the sites are significantly lower than the sites of cluster A ($t=2.64$, $DF=11$ $P<0.05$), there is no difference in pH. The sites of this cluster lie on a variety of soil types derived from either boulder clay or mineral origins. No site is on deep peat. The vegetation varies; in some sites *Juncus spp.* dominate (e.g. site 7), whereas in sites 14 and 11, *Deschampsia spp.* and *Molinia caerulea* respectively are more abundant. Sites 18 and 19 have a mixture of these types. No site is dominated by *Calluna vulgaris* which is confined to deep peat sites. The heights and densities of the ground vegetation vary among the sites, ranging from no ground vegetation under the thinned Norway Spruce (site 20) to the tall, dense swards of the unplanted sites 17 and 18.

The immediate surroundings of the sites vary greatly and include an alder wood (site 18), calcifugous grasslands (site 16), a reservoir edge (site 17), a roadside verge (site 11) and the banks of a river (site 7). The latter two are both adjacent to closed canopy forests. Sites directly associated with forestry practices are, a thinned Norway Spruce plantation (site 20), a clearfell site (site 19), and two young restock sites (sites 14 and 13)

The indicator species of community C2 are *Carabus violaceus*, *C.problematicus*, *Leistus rufescens*, *Notiophilus biguttatus*, *Loricera pilicornis*, *Pterostichus madidus*, *P.niger*, *Calathus micropterus*, *Agonum fuliginosum* and *Amara lunicollis*. Of these, only *Amara lunicollis* is exclusive to cluster B, and therefore a reliable indicator of community C2. This fits the description given by Lindroth (1985) that it is a species of dry open country. *Agonum fuliginosum* and *Loricera pilicornis* are almost exclusive to the cluster, but are found in only a few of the sites. However,

Butterfield and Coulson (1983) found that both these species formed part of their deep peat association in northern England. This also included the three indicator species of deep peat soils found in this study. Consequently, the use of these beetles as indicators of the shallow peat and mineral soil habitats of community C2 may be unreliable. Another species which is nearly exclusive to the cluster is *Calathus micropterus*. Butterfield and Coulson (1983) indicate that it is characteristic of shallow peat sites in northern England. In the present study it was rare among the shallow peat sites within this cluster but abundant at site 20, where 353 individuals were caught. This huge bias towards one site is inconsistent with the beetle's suggested preference of shallow peat soils and it cannot be considered a reliable indicator of community C2.

Another group of carabids were more widely distributed among the sites of cluster B than the former species. This group included *Pterostichus niger* which was found throughout all the sites in the cluster, whereas only a single specimen was recovered from cluster A sites. It appears to be a reliable indicator of community C2. Two species widespread amongst the sites of class B, but less exclusive to it, were *Carabus problematicus* and *Notiophilus biguttatus*. They could be useful indicators of the characteristic habitat of community C2 only if in conjunction with other species.

Finally, there is a set of indicator species which were caught in generally higher numbers in community C2 than in C1 but are still present elsewhere. These are *Carabus violaceus*, *Leistus rufescens* and *Pterostichus madidus*. The average numbers per site in cluster B were significantly greater than in cluster A with respect to *Carabus violaceus* ($t=2.49$, $DF=8$, $P<.05$) and *Leistus rufescens* ($t=2.33$, $DF=8$, $P<.05$). This was not so for *Pterostichus madidus*.

Pterostichus madidus is not a reliable indicator of community C2 and *Carabus*

violaceus should be used with care as it was found to be widespread among peat sites of other areas of northern England by Butterfield and Coulson (1983). *Leistus rufescens* is not known as a species common on peat soils and in view of its abundance in the pitfall catches of cluster B, it is a reliable indicator of the habitat of community C2.

Therefore, individually, only *Leistus rufescens*, *Amara lunicollis* and *Pterostichus niger* are reliable indicators of the carabid community of open areas in Kielder on shallow peat or mineral soils. However, if all the species of community C2 are considered together, a very reliable indication of the community can be made. Any new sites found to have this community can be slotted into cluster B with confidence because it is absent from the deep peat sites of cluster A and the closed canopy forest sites of clusters C,D and E.

SITE 21- Lower altitude site on a river bank

Site 21 is at a relatively low altitude of 250m a.s.l., it has relatively alkaline soils of pH 5.8, and is situated on the banks of a river within a grazed pasture.

Of all the sites in Kielder, site 21 contained more species and more individuals of carabids than any other. Although enough of the indicator species of community C2 were captured to suggest that it is represented at this site, the CLUSTAN dendrogram places it separately. This is because additional species were caught in large numbers and these may form the basis of another community recurrent in other similar sites. Some of these species, such as *Agonum muelleri*, *Pterostichus versicolor* and *P. melanarius*, are species associated with open areas with short vegetation (Lindroth 1985) whilst others, such as *Pterostichus vernalis*, *Elephras cupreus* and *Carabus granulatus*, are species associated with river banks. The characteristics of this

local environment has produced a carabid fauna unlike any other sampled site in Kielder.

CLUSTERS C,D AND E.- The closed canopy forest sites

Most of the sites in clusters C, D and E are within closed canopy blocks of Sitka Spruce which lack continuous ground vegetation. Only occasional ferns and sparse amounts of moss persist. Instead is a thick carpet of shed needles. These sites occur at a mean altitude of 321 (+/- 17m) a.s.l. The two sites of cluster E are slightly different, being associated with larch rather than spruce and are at a lower altitude of 210m. Site 9 from this cluster, is on a roadside verge adjacent to the larch block where the vegetation is tall and species-rich. It is not representative of the closed canopy forest clusters and will not be considered further.

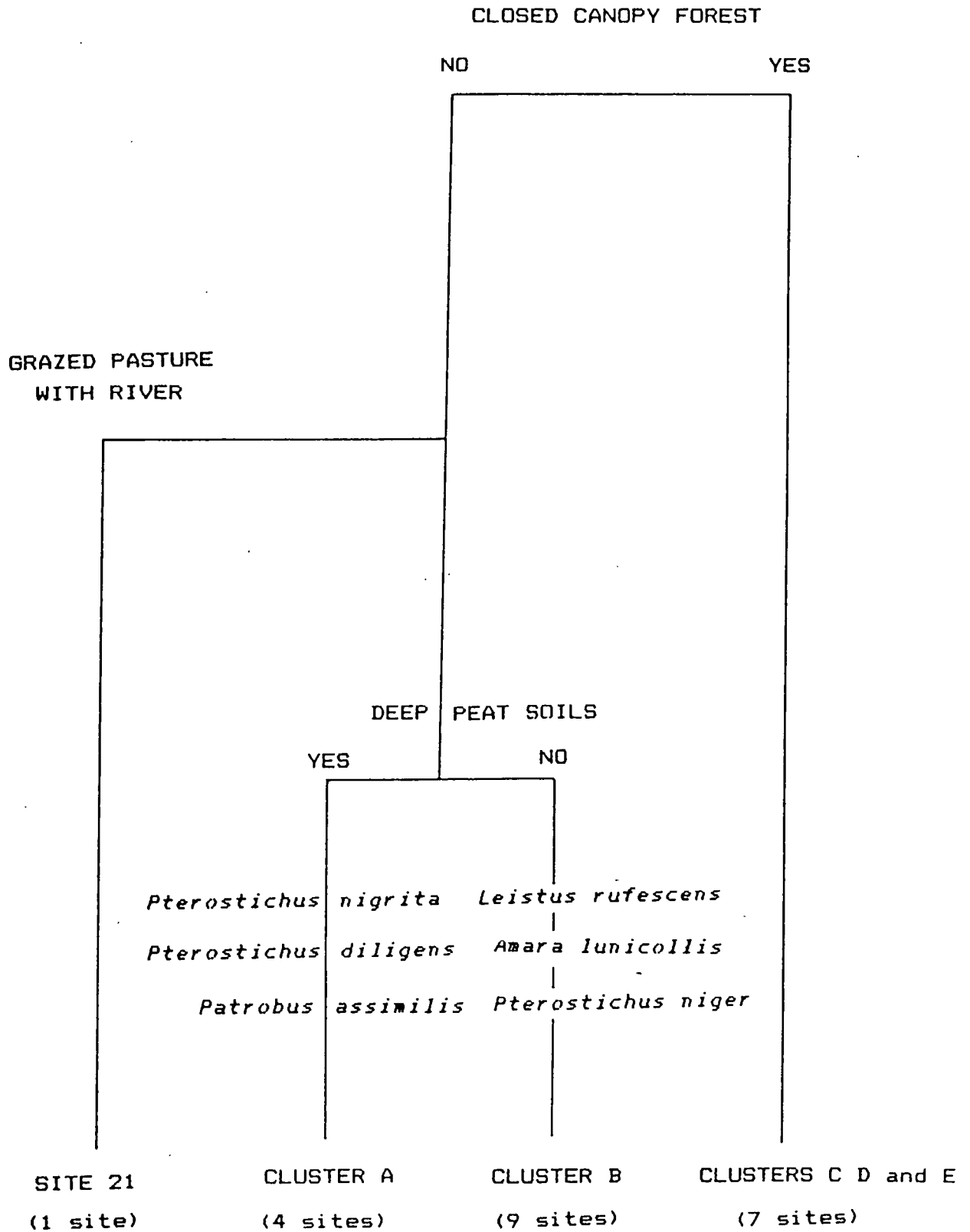
Cluster C contains the three most impoverished sites sampled in terms of the carabid fauna. Overall, 19 specimens of *Patrobus assimilis* were caught here and only single specimens of other species. In the sites of Cluster D, *Trechus obtusus*, *Patrobus assimilis* and *Trechus rubens* were frequently found, but little else was caught. Numbers of species were too low to suggest any identifiable communities existing in these sites, only tolerant species from the surrounding communities remaining. *Pterostichus nigrita* and *P.diligens* were absent despite being indicator species of cluster A sites, three of which are within 10 metres of these forest sites.

Site 10, from cluster E, was less impoverished in terms of the numbers of carabids caught, but most of the individuals were of one species, *Trechus secalis*.

CONCLUSION

Overall, it appears that the overriding environmental factor affecting the Carabidae within Kielder Forest is the presence or absence of a closed canopy. In open areas the carabid communities largely respond to the presence or absence of deep peat soils, although other communities may exist in sites with special characteristics such as in pastures on river banks. This is summarised in Figure 3a.

Figure 3a Summary Dendrogram showing the 3 main CLUSTAN clusters, with Indicator Species for the Carabidae



CHAPTER 4

THE EFFECTS OF AFFORESTATION ON CARABIDAE

Afforestation may change the environment in several ways;

- i) Draining or ploughing the ground prior to planting may affect the hydrology of the site. The water-table is usually lowered causing the site to become drier, with localised increases in moisture only where drainage ditches empty.
- ii) Trees take up further ground moisture through evapo-transpiration. This may lead to further dessication and lowering of the water-table.
- iii) After 10-15 years, dependent on species planted and physical conditions, the canopy will close, light will be excluded from the forest floor and the number of plant species present will be reduced.

The first part of this chapter investigates how some of these changes resulting from afforestation, may affect the carabid fauna. To gain a comprehensive picture of the effects of afforestation one must consider how the community of animals changes through a forest cycle. This would ideally be achieved with a long term study lasting from initial preparation of the site prior to planting until canopy closure of the second rotation or restock. This is not practical for many reasons. As a substitute, temporal variations were considered by studying different aged stands in a spatially varying context. Six matched pairs of afforested and adjacent unafforested sites were studied in this manner. Apart from sites 20 and 17, all pairs of sites were within 10 metres of each other.

The paired comparisons were used to test the prediction that the carabid community of open unafforested areas will have a lower species diversity than equivalent afforested areas. Three aspects of carabid community structure were measured for each of the paired sites (Table 4a); species richness (the number of species caught), the number of individuals caught and an index of species diversity (the percentage of individuals comprised by the five most abundant species).

There was no significant difference in the number of individuals caught between unafforested and afforested sites, but significantly fewer species were caught in afforested sites than in the paired unafforested sites ($t=3.72$, $df=5$, $p<0.05$). This supports the prediction made that afforestation lowers the number of species present, but tells us little about why this decrease has occurred and which species are excluded.

To provide more detailed information on how afforestation reduces the number of species, it is essential to know more about the species that are excluded. To this end, each species was categorised according to whether they are:

- i) Moisture loving ("moist") or dry loving ("dry") species.
- ii) Shade tolerant species or species only found in open conditions.
- iii) Adult overwintering species or larval overwintering species.

The above categorisations were derived using information presented in den Boer (1977), Lindroth (1974, 1985 and 1986), Murdoch (1967) and Turin and den Boer (1988) and is presented for each species in Table 4b. Where inconsistencies arose, the

Table 4a. Measurements of carabid community structure in matched pairs of afforested and adjacent unafforested sites. Diversity is expressed as the percentage of the catch comprised by the five most abundant species at each site.

| Afforested sites | | | | Unafforested sites | | | |
|----------------------|---------------|----------------|----------------------|----------------------|---------------|----------------|----------------------|
| Site | No.of Species | No.of Individ. | % top 5spp. to total | Site | No.of Species | No.of Individ. | % top 5spp. to total |
| 2 | 2 | 12 | 100 | 1 | 8 | 57 | 95 |
| 4 | 5 | 25 | 100 | 3 | 7 | 34 | 94 |
| 6 | 2 | 4 | 100 | 5 | 8 | 64 | 92 |
| 8 | 3 | 9 | 100 | 7 | 15 | 52 | 77 |
| 10 | 8 | 106 | 96 | 9 | 10 | 310 | 98 |
| 20* | 12 | 537 | 97 | 17* | 23 | 121 | 64 |
| Total Species = 24 | | | | Total Species = 31 | | | |
| Total Individ. = 691 | | | | Total Individ. = 638 | | | |

* Unpaired sites, but closest "pair" in terms of distance and site characteristics.

Table 4b. The division of carabid species into ecological groups according to their habitat preferences, life history patterns and mobility.

| | HABITAT PREFERENCES | | | LIFE HISTORY | | POTENTIAL MOBILITY | |
|--------------------------------|---------------------|-----|-----------|----------------|------------------------------|--------------------|-----|
| | MOIST | DRY | OPEN ONLY | SHADE TOLERANT | OVERWINTER AS: ADULTS LARVAE | HIGH (Opportunist) | LOW |
| <u>Cychnus caraboides</u> | | X | | X | X | | X |
| <u>Carabus glabratus</u> | | X | | X | X | | X |
| <u>C.problematicus</u> | | X | | X | X | | X |
| <u>C.violaceus</u> | | X | | X | X | | X |
| <u>Leistus rufescens</u> | | X | | X | X | | X |
| <u>Nebria gyllenhali</u> | X | | | | | | |
| <u>N.salina</u> | | X | X | | X | | X |
| <u>Notiophilus aquaticus</u> | X | | | | X | | X |
| <u>N.biguttatus</u> | | X | | X | X | X | |
| <u>N.palustris</u> | X | | | X | X | | X |
| <u>Loricera pilicornis</u> | X | | | X | X | X | |
| <u>Dyschirius globosus</u> | X | | X | X | X | | X |
| <u>Patrobus assimilis</u> | X | | | X | X | | X |
| <u>P.atrorufus</u> | | X | | X | X | | X |
| <u>Trechus obtusus</u> | | X | | X | X | | X |
| <u>T.rubens</u> | X | | | X | X | X | |
| <u>T.secalis</u> | X | | | X | X | | X |
| <u>Bembidion bruxellense</u> | X | | | X | X | X | |
| <u>B.unicolor</u> | X | | | X | X | | X |
| <u>Pterostichus adstrictus</u> | X | | | X | X | X | |
| <u>P.diligens</u> | X | | | X | X | | X |
| <u>P.madidus</u> | | X | | X | X | | X |
| <u>P.niger</u> | X | | | X | X | | X |
| <u>P.nigrita</u> | X | | | X | X | X | |
| <u>P.strenuus</u> | X | | | X | X | X | |

continued

Table 4b continued

| | MOIST | DRY | OPEN ONLY | SHADE TOLERANT | OVERWINTER AS: ADULTS | LARVAE | POTENTIAL MOBILITY HIGH | POTENTIAL MOBILITY LOW |
|-------------------------------|-------|-----|-----------|----------------|--------------------------|--------|----------------------------|---------------------------|
| <u>Abax parallelepipedus</u> | | X | | X | X | X | | X |
| <u>Calathus micropterus</u> | | X | | X | X | X | | X |
| <u>Agonum albipes</u> | X | | | | X | X | X | |
| <u>A.fuliginosum</u> | X | | | X | X | X | X | |
| <u>Amara aulica</u> | X | | X | | X | X | X | |
| <u>A.communis</u> | | X | X | | X | X | X | |
| <u>A.lunicollis</u> | | X | X | X | X | X | X | |
| <u>Trichocellus placidus</u> | X | | | X | X | X | X | |
| <u>Agonum versutum</u> | X | | X | X | X | X | X | |
| <u>Pterostichus cristatus</u> | X | | | | X | X | | X |
| <u>Bradycellus harpalinus</u> | | X | X | X | X | X | X | |

category assigned by the author who studied the nearest equivalent area to Kielder was chosen.

To evaluate the effects of afforestation on the proportion of species within each of the categories, the following null hypotheses were formed;

There is no difference in the proportion of;

- i) "dry" species,
- ii) species preferring open sites, and
- iii) larval overwintering species

caught in afforested and unafforested sites.

The null hypotheses were tested by comparing the above proportions which are expressed as percentages in figure 4a using chi-squared analysis. A significantly higher proportion of "dry" species were found in afforested areas (66%) than in unafforested areas (35%) (Chi-squared =7.9, df=1, $p < 0.01$). This difference may arise in one of two ways; either the number of "dry" species is higher in afforested areas than unafforested areas or conversely, the number of "moist" species is lower. It can be seen from Table 4c that fewer "moist" species were found in afforested sites, whereas the incidence of "dry" species is similar.

Table 4c. The number of carabid species which prefer either moist or dry conditions caught in afforested and unafforested sites.

| | Afforested | Unafforested | Total |
|-----------------|------------|--------------|-------|
| "Dry" species | 18 | 20 | 38 |
| "Moist" species | 12 | 47 | 59 |
| Total | 30 | 67 | 97 |

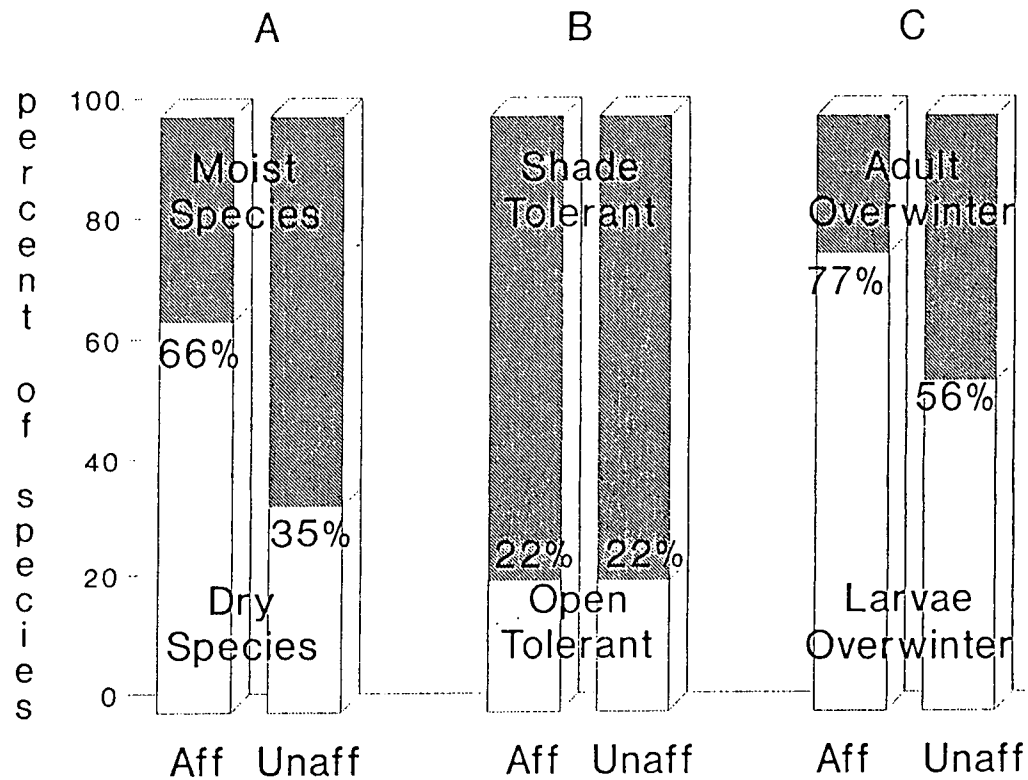


Figure 4a. The percentage of carabid species within the ecological categories;

A: Species preferring either dry or moist sites,

B: Shade (forest) tolerant species and those in open sites only,

C: Species which overwinter either as larvae or as adults,

for afforested and unafforested sites in Kielder Forest.

Thus, it appears that afforestation acts by reducing the number of species associated with moist environments rather than by increasing the absolute number of species tolerant of dry conditions. When numbers of individuals caught were considered, a very similar pattern emerged, with 84% of individuals caught in afforested areas being "dry" species as opposed to only 17% in unafforested areas (Chi-squared=630, df=1, $p<0.001$).

The percentage of species preferring open conditions was equal (22%) in each set of sites, whilst the proportion of species overwintering as larvae was significantly higher in afforested sites (77%) than in unafforested sites (56%) (Chi-squared = 5.7, df=1, $p<0.05$) (Table 4d).

Table 4d. The number of species of carabids which overwinter as larvae or as adults in afforested and unafforested sites.

| | Afforested | Unafforested | Total |
|-------------------|------------|--------------|-------|
| Larvae overwinter | 24 | 42 | 66 |
| Adult overwinter | 5 | 31 | 36 |
| Total | 29 | 73 | 102 |

The magnitude of this difference was increased when the number of individuals caught was considered, with 98% of animals caught in afforested sites being species that overwinter as larvae compared to 74% in unafforested sites (Chi-squared = 186, df=1, $p<0.001$).

Thus null hypotheses i) and iii) are rejected. Afforestation appears to affect the carabid community by increasing the proportion of species tolerant of dry conditions through reducing the suitability of the habitat for "moist" species and by

increasing the proportion of species that overwinter in a larval stage. As there was no difference in the proportion of species preferring open conditions, null hypothesis ii) cannot be rejected.

The second part of this chapter considers the opportunistic capacity and the mobility of the carabid community. The overriding question under consideration is whether the original carabid community present in open conditions prior to planting will recolonise in the relatively short time available when conditions are once again suitable, ie. between clearfelling and canopy closure of the second rotation trees.

It is predicted that the carabid community on clearfell and young second rotation areas will contain more ruderal or opportunistic species than the community on open unafforested sites. However, the carabid fauna after clearfelling may differ from that on original unafforested areas due to the former having been drained prior to planting. These drains may not be blocked and may still influence the hydrology of the site. Hence, a second prediction is made; "moist" species will be fewer on clearfelled and second rotation sites than on unafforested sites.

These predictions were tested by comparing the carabid faunas caught in pitfall traps at two early second rotation sites (sites 13 and 14) and at a clearfell site (site 19) with three similar unplanted sites (sites 16, 17 and 18). The opportunistic potential of each species was assessed from a review of the relevant literature. Where no reference to a species' status was given, an assessment of opportunistic potential was extrapolated from records of their mobility. An opportunistic species was classed as one tending to be highly mobile. Winged species and dimorphic species with a high proportion of winged individuals were categorised as mobile opportunists, whereas wingless species or dimorphic species with a low proportion of winged individuals were categorised as low mobile, low opportunists (Table 4b).

The following two null hypotheses were formed to test the predictions made that there is no difference in the proportion of;

i) opportunistic species, and

ii) "moist" species

between open unafforested sites and otherwise similar clearfell and early second rotation sites.

Chi-squared tests were used to assess potential differences. No significant differences were found between either the proportion of opportunistic species in unafforested sites (55%) and second rotation sites (49%), or between the proportion of "moist" species in unafforested sites (58%) and second rotation sites (51%). Thus, neither of the null hypotheses can be rejected and it can be concluded that for Carabidae, a completed forestry cycle does not appear to result in fewer "moist" species and more opportunistic species in the communities present on early restock sites relative to areas that have not been forested.

CONCLUSION

I conclude that the community of carabids is adversely affected by afforestation in that the species which prefer moist habitat conditions and those that overwinter as adults are largely excluded from the forested environment resulting in a lower occurrence of species. However, the original community quickly returns to the temporary open areas of clearfell and young restocks within the forestry rotation.

CHAPTER 5

CARABIDS AS INDICATORS OF GENERAL INVERTEBRATE COMMUNITIES

Carabids are likely to be good indicators of general invertebrate communities if:

a)they follow the same trends of abundance among the clusters identified by the carabid communities (carabid clusters) as do other invertebrate groups. Hence, clusters with many carabids should show high levels of abundance of other invertebrates and those with fewer carabids should have low levels of abundance of these groups,

b)the classification of invertebrate group data by CLUSTAN does not contradict that of the carabid classification.

These conditions have been investigated using data shown in Appendix 2 and 3, based on other invertebrate groups obtained by sampling with pitfall traps and soil extraction methods.

INVERTEBRATES SAMPLED BY PITFALL TRAPPING.

There appear to be parallels in the abundance of carabids and other invertebrate groups among the carabid clusters. Table 5a shows the mean numbers of individuals of each taxonomic group per site and the total mean of all groups for each carabid cluster. The respective number of carabids are included for comparison.

Table 5a. The mean number (+/- 1S.E.) of invertebrates per site in each carabid class defined by CLUSTAN.

| CLASS | A (4 sites) | B (9 sites) | 21 (1 site) | C (3 sites) | D (2 sites) | E (2 sites) |
|-------------------|----------------|----------------|----------------|----------------|----------------|----------------|
| CARABIDAE | 45 +/- 9 | 255 +/- 70 | 600 | 7 +/- 2 | 17 +/- 7 | 208 +/- 72 |
| Nematocera | 334 +/- 60 | 393 +/- 159 | 51 | 232 +/- 188 | 293 +/- 115 | 669 +/- 174 |
| Tipulidae | 50 +/- 15 | 52 +/- 19 | 6 | 29 +/- 6 | 235 +/- 6 | 41 +/- 2 |
| Other Diptera | 8 +/- 8 | 211 +/- 45 | 199 | 68 +/- 30 | 66 +/- 22 | 390 +/- 132 |
| Diptera larv. | 11 +/- 3 | 25 +/- 5 | 18 | 12 +/- 2 | 11 +/- 7 | 7 +/- 2 |
| Staphylinidae | 108 +/- 16 | 235 +/- 59 | 178 | 108 +/- 29 | 112 +/- 7 | 505 +/- 163 |
| Other Coleoptera | 45 +/- 7 | 199 +/- 52 | 206 | 61 +/- 25 | 52 +/- 25 | 386 +/- 123 |
| Coleoptera larv. | 48 +/- 23 | 66 +/- 16 | 82 | 17 +/- 5 | 11 +/- 2 | 70 +/- 20 |
| Hymenoptera | 468 +/- 268 | 267 +/- 110 | 277 | 24 +/- 12 | 63 +/- 53 | 178 +/- 116 |
| Lepidoptera larv. | 10 +/- 4 | 24 +/- 11 | 1 | 2 +/- 2 | 2 +/- 2 | 12 +/- 3 |
| Hemiptera | 72 +/- 24 | 113 +/- 45 | 85 | 28 +/- 5 | 40 +/- 21 | 39 +/- 14 |
| Araneae | 211 +/- 29 | 511 +/- 56 | 9 | 159 +/- 16 | 173 +/- 71 | 569 +/- 92 |
| Opiliones | 17 +/- 7 | 172 +/- 51 | 9 | 22 +/- 12 | 22 +/- 13 | 75 +/- 17 |
| Isopoda | 0 | 17 +/- 10 | 2 | 0 | 0 | 13 +/- 2 |
| Chilo./ Diplopoda | 6 +/- 2 | 55 +/- 31 | 3 | 10 +/- 8 | 16 +/- 14 | 45 +/- 17 |
| "Slugs" | 24 +/- 24 | 32 +/- 14 | 27 | 2 +/- 1 | 2 +/- 1 | 6 +/- 3 |
| Annelids | 4 +/- 4 | 19 +/- 6 | 34 | 1 +/- 1 | 2 +/- 2 | 10 +/- 2 |
| TOTAL INVERTS. | 1356 +/- 308 | 2696 +/- 413 | 2615 | 753 +/- 315 | 905 +/- 103 | 3244 +/- 91 |

More invertebrates were found in cluster B sites than cluster A. ($t=2.59$, $DF=11$ $P<0.05$). This trend was the same for each individual invertebrate group except for Hymenoptera, with significant differences for Araneae ($t=4.79$, $DF=11$ $P<0.01$), and Coleoptera (excepting Staphylinidae and Carabidae) ($t= 2.95$, $DF=11$ $P<0.05$).

As with the carabids, significantly fewer invertebrates were caught below closed canopy forest (sites of clusters C,D and E) than in open areas (sites of clusters A and B) ($t= 2.89$ $DF=19$ $P<0.05$). This is with the exclusion of site 9 from the forested clusters which was thought to be misclassified in the carabid analysis. The difference was greatest between the forested sites and cluster B. In fact, some groups such as Opiliones, Chilopoda and Diplopoda and Coleoptera (other than Staphylinidae and Carabidae), were equally abundant in the clusters below closed canopy forestry as they were in the sites of cluster A.

Site 21 produced a high total number of invertebrates (2615 individuals) and a high carabid total. However, although this site was favourable for Coleoptera, Hemiptera and Lumbricidae, other groups such as Nematocera, Araneae and Opiliones, were poorly represented and it is assumed that the preferred conditions for these groups were not present within this site.

Overall, the trends in the abundance of invertebrates among the carabid clusters conforms well to that of the carabids with only minor inconsistencies. Furthermore, the major invertebrate groups can be shown to vary consistently in abundance among the sites. Table 5b shows this tabulatively and table 5c depicts the correlation coefficients between the groups which are all significant and positive. It would appear that carabids are reliable indicators of the trends in the abundances of other invertebrates caught in pitfall traps and therefore fulfil the first condition stipulated for reliable indicators.

Table 5b. The total number of four major groups of invertebrates caught in pitfall traps at 21 sites in Kielder Forest in 1988.

| | Site Number | | | | | | | | | | |
|------------------------|-------------|-----|-----|-----|-----|-----|-----|-----|------|------|------|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 |
| Araneae | 228 | 166 | 125 | 101 | 238 | 127 | 408 | 244 | 682 | 456 | 611 |
| Opiliones | 15 | 15 | 13 | 35 | 1 | 5 | 15 | 8 | 95 | 54 | 26 |
| Coleoptera (adults) | 218 | 139 | 141 | 225 | 241 | 120 | 222 | 141 | 1558 | 715 | 650 |
| Diptera (adults) | 211 | 201 | 252 | 526 | 238 | 133 | 114 | 239 | 1477 | 722 | 883 |
| Total | 672 | 521 | 531 | 887 | 718 | 385 | 759 | 632 | 3812 | 1947 | 2170 |

continued...

| | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 |
|------------------------|------|-----|------|-----|------|------|------|------|------|------|
| Araneae | 183 | 275 | 386 | 251 | 542 | 782 | 572 | 673 | 348 | 816 |
| Opiliones | 45 | 8 | 79 | 36 | 377 | 287 | 385 | 234 | 140 | 9 |
| Coleoptera (adults) | 283 | 314 | 465 | 197 | 745 | 1086 | 860 | 1077 | 1324 | 1005 |
| Diptera (adults) | 754 | 223 | 383 | 447 | 1714 | 535 | 890 | 388 | 534 | 256 |
| Total | 1265 | 820 | 1313 | 931 | 3378 | 2690 | 2707 | 2302 | 2346 | 2086 |

Table 5c. Correlation matrix for the major invertebrate groups caught in 21 sets of pitfall traps in Kielder Forest.

| | Araneae | Opiliones | Coleoptera | Diptera |
|------------|---------|-----------|------------|---------|
| Araneae | - | 0.54 * | 0.81 *** | 0.44 * |
| Opiliones | | - | 0.55 * | 0.60 ** |
| Coleoptera | | | - | 0.56 ** |
| Diptera | | | | - |

* P<0.05, ** P<0.01, *** P<0.001

The second condition can be considered by reviewing the results of a CLUSTAN classification of the sites using invertebrate groups caught by pitfall traps. Figure 5a shows the dendrogram produced from this classification. At the level of similarity of .83, above which the clusters cannot be interpreted, there are two main invertebrate clusters and one single site.

Table 5d shows the abundance of each invertebrate group among their clusters. This is expressed in terms of pseudospecies. The higher the pseudospecies value, the more abundant the group of invertebrate. The 8 sites within cluster Z all have high numbers of invertebrates. These sites are all open in terms of forest canopy, mainly belonging to cluster B of the carabid analysis. Sites 21 and 9 come from other carabid clusters but neither site lies directly beneath forest canopy. Conversely, fewer invertebrates were caught from cluster X sites. This includes all the closed canopy forest sites of carabid clusters C, D and E (except site 6), all of carabid cluster A and three sites from carabid cluster B (7, 13 and 14). All these sites are closely associated with the plantations, being either closed canopy forest sites, restock sites, or sites in rides or on river banks within plantations. Only the moorland site (site 15) is included which is disassociated from the forest.

Site 6 is separated from the rest of the sites because of the extremely low numbers of invertebrates captured. Table 5d shows the pseudospecies values at this site to be lowest for each group other than Lumbricidae.

The classification of sites by pitfall trapped invertebrates is based solely on numbers of invertebrates, predominantly separating open sites with high numbers of invertebrates from forestry associated sites with lower numbers of invertebrates. To investigate whether any other patterns could be found, a DECORANA analysis was run,

Figure 5a. The Classification of Sites by CLUSTAN using the Composition of Invertebrate Groups.

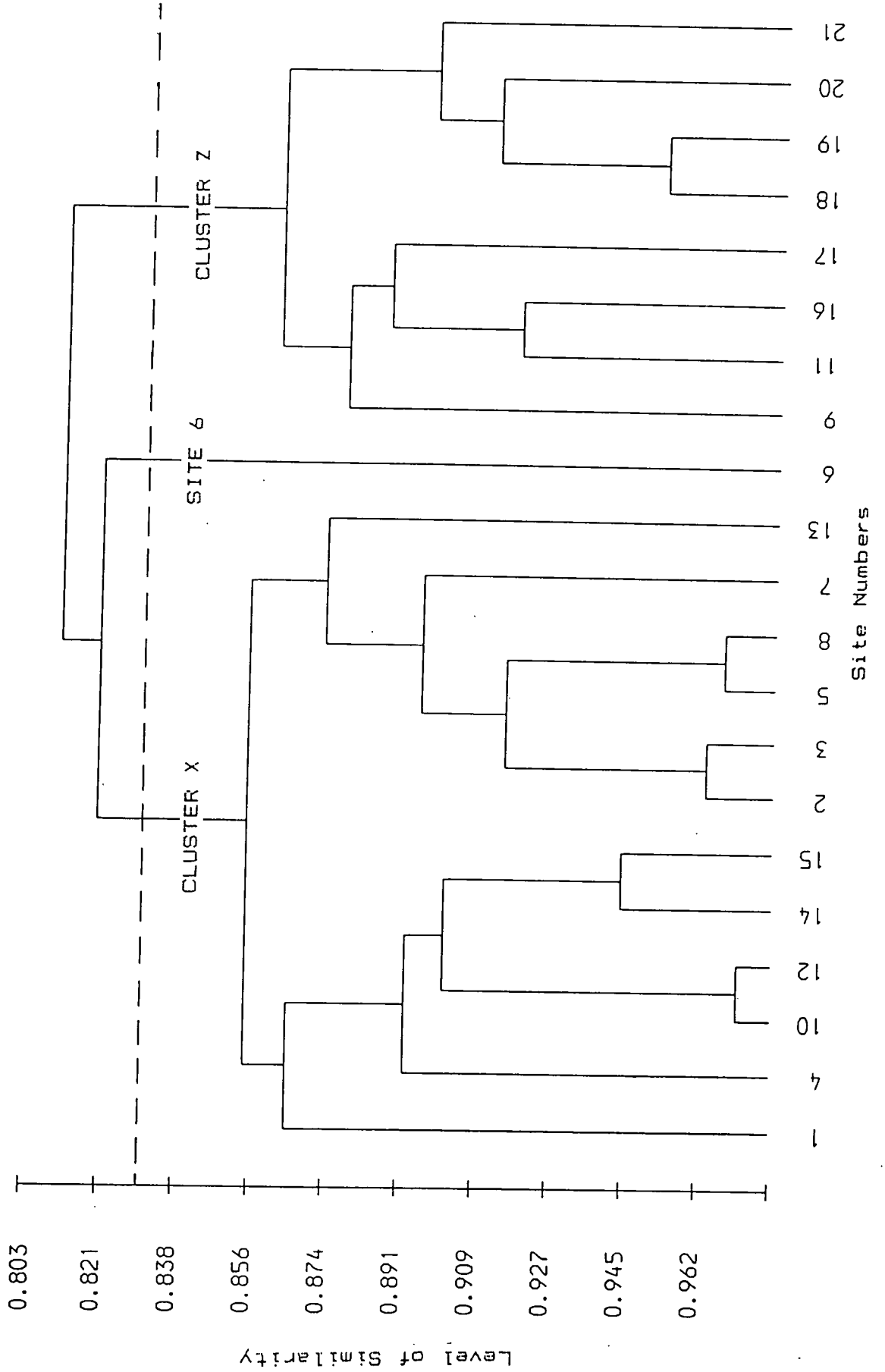


Table 5d. The abundances of invertebrate groups caught at each site and ordered by the Clustan classification. Abundances are represented as pseudospecies values; 1 (1 - 4 individuals), 2 (5 -149), 3 (150 - 749), 4 (>750), - (not caught).

| CLUSTAN CLASS | X | | | | | | | | | | | | | | | | | | | | | Y | Z | | | | | | | | | | | | | | | | | | | | |
|--------------------|---|---|----|----|----|----|---|---|---|---|---|----|---|---|----|----|----|----|----|----|----|---|---|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|
| | 1 | 4 | 10 | 12 | 14 | 15 | 2 | 3 | 5 | 8 | 7 | 13 | 6 | 9 | 11 | 16 | 17 | 18 | 19 | 20 | 21 | | | | | | | | | | | | | | | | | | | | | | |
| SITE NUMBER | 1 | 4 | 10 | 12 | 14 | 15 | 2 | 3 | 5 | 8 | 7 | 13 | 6 | 9 | 11 | 16 | 17 | 18 | 19 | 20 | 21 | | | | | | | | | | | | | | | | | | | | | | |
| Diptera | 2 | 2 | 3 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | | | | | | | | | | | | | | | | | | | | | | |
| Staphylinidae | 2 | 2 | 3 | 3 | 3 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | | | | | | | | | | | | | | | | | | | | | | |
| Carabidae | 2 | 2 | 2 | 1 | 3 | 2 | 2 | 2 | 2 | 1 | 2 | 3 | 1 | 3 | 3 | 3 | 2 | 3 | 3 | 3 | 3 | | | | | | | | | | | | | | | | | | | | | | |
| Other Coleopetra | 2 | 2 | 3 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 3 | 2 | 3 | 3 | 3 | 3 | 3 | 3 | | | | | | | | | | | | | | | | | | | | | | |
| Araneae | 3 | 2 | 3 | 3 | 3 | 3 | 3 | 2 | 3 | 3 | 3 | 3 | 2 | 3 | 3 | 3 | 4 | 3 | 3 | 3 | 4 | | | | | | | | | | | | | | | | | | | | | | |
| Hemiptera | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 3 | 3 | 2 | 2 | 2 | 2 | | | | | | | | | | | | | | | | | | | | | | |
| "Worms" | 2 | 1 | 1 | 1 | 1 | 2 | 1 | - | 1 | 1 | - | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 2 | 2 | 2 | | | | | | | | | | | | | | | | | | | | | | |
| "Snails" | 2 | 1 | 1 | 1 | 1 | 2 | 2 | - | 1 | 1 | 1 | 1 | - | 1 | 1 | 1 | 2 | 2 | 1 | - | 1 | | | | | | | | | | | | | | | | | | | | | | |
| Slugs | 2 | 1 | 1 | 1 | 1 | 2 | 2 | - | 1 | 1 | 1 | 1 | - | - | 2 | 1 | 2 | 2 | 2 | 1 | 2 | | | | | | | | | | | | | | | | | | | | | | |
| Opiliones | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 3 | 3 | 3 | 3 | 2 | 1 | | | | | | | | | | | | | | | | | | | | | | |
| Nematocera | 2 | 3 | 3 | 3 | 3 | 3 | 2 | 2 | 2 | 3 | 2 | 2 | 2 | 4 | 3 | 4 | 2 | 3 | 3 | 2 | 2 | | | | | | | | | | | | | | | | | | | | | | |
| Hymenoptera | 3 | 1 | 2 | 2 | 2 | 2 | 2 | 2 | 4 | 2 | 3 | 3 | 1 | 3 | 4 | 3 | 3 | 2 | 2 | 2 | 3 | | | | | | | | | | | | | | | | | | | | | | |
| Lepidoptera larvae | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 2 | 2 | 1 | 1 | 1 | 1 | | | | | | | | | | | | | | | | | | | | | | |

but the taxa and sample scores cannot be interpreted conclusively. As the trends of abundance of each group are similar between sites, the variation in invertebrate numbers between sites will not show up on a DECORANA axis. The next most important factors influencing the site and taxa ordinations must be weak.

Although the classification produced from the invertebrate group data is different to that of the carabid classification, it does not contradict it. No other major influence on the classification could be found apart from numbers of invertebrates in the sites and this varies in the same way as the carabids. Therefore, the second condition holds true and carabids are likely to be good indicators of general invertebrate communities. However, communities of invertebrate species must be found and compared with the distribution of the carabid communities, before this can be verified completely.

INVERTEBRATES EXTRACTED FROM SOIL SAMPLES (SOIL INVERTEBRATES)

There appear to be few parallels in the trends of abundance of carabids and soil invertebrates among the carabid clusters. This is depicted in table 5e which shows the mean densities per site of each taxonomic group and the total mean of all groups for each carabid cluster. The respective number of carabids are included for comparison.

From the total soil invertebrate values, it can be seen that there are three major differences in the trends shown by the mean densities of soil invertebrates among the carabid clusters when compared to the trends shown by the carabids.

- 1) Carabid abundance appears to be affected more by closed canopy forest conditions than the abundance of soil invertebrates. Clusters C and D, which lie below a closed

Table 5e. The mean number of soil invertebrates (+/- 1S.E.) extracted from a 5 m2 soil sample per site within each carabid cluster.

* The mean number of carabids caught in pitfall traps per site within each cluster are included for comparison.

| | CLUSTER A | CLUSTER B | SITE21 | CLUSTER C | CLUSTER D | CLUSTER E |
|--------------------------|--------------|---------------|--------|---------------|--------------|--------------|
| CARABIDAE * | 45 +/- 9 | 255 +/- 70 | 600 | 7 +/- 2 | 17 +/- 7 | 208 +/- 72 |
| Nematocera | 1058 +/- 872 | 517 +/- 206 | 92 | 1392 +/- 798 | 388 +/- 249 | 139 +/- 31 |
| Other Diptera | 18 +/- 7 | 23 +/- 7 | 36 | 58 +/- 48 | 85 +/- 8 | 14 +/- 14 |
| Diptera larv. | 2875 +/- 478 | 1965 +/- 520 | 1145 | 1492 +/- 257 | 1132 +/- 393 | 896 +/- 141 |
| Carabidae | 73 +/- 17 | 81 +/- 23 | 0 | 6 +/- 6 | 37 +/- 37 | 16 +/- 16 |
| Staphylinidae | 609 +/- 75 | 750 +/- 193 | 172 | 250 +/- 55 | 309 +/- 4 | 588 +/- 187 |
| Other Coleoptera | 39 +/- 22 | 143 +/- 56 | 261 | 17 +/- 17 | 25 +/- 7 | 69 +/- 39 |
| Coleoptera larv. | 1074 +/- 492 | 983 +/- 223 | 113 | 1078 +/- 372 | 1488 +/- 492 | 674 +/- 60 |
| Hymenoptera | 148 +/- 79 | 101 +/- 46 | 119 | 21 +/- 14 | 0 | 30 +/- 30 |
| Lepidoptera larv. | 14 +/- 9 | 30 +/- 9 | 61 | 0 | 0 | 8 +/- 8 |
| Hemiptera | 195 +/- 95 | 107 +/- 45 | 0 | 5 +/- 4 | 445 +/- 44 | 15 +/- 15 |
| Araneae | 145 +/- 45 | 317 +/- 98 | 36 | 247 +/- 50 | 504 +/- 137 | 250 +/- 35 |
| Opiliones | 14 +/- 8 | 124 +/- 44 | 0 | 0 | 0 | 16 +/- 16 |
| Isopoda | 0 | 136 +/- 85 | 19 | 0 | 0 | 33 +/- 14 |
| Chilo./Diplopoda | 18 +/- 18 | 75 +/- 44 | 0 | 93 +/- 75 | 0 | 38 +/- 23 |
| "Slugs" | 13 +/- 9 | 39 +/- 16 | 18 | 18 +/- 18 | 0 | 36 +/- 36 |
| Annelids | 108 +/- 50 | 758 +/- 211 | 1464 | 94 +/- 23 | 188 +/- 54 | 209 +/- 178 |
| Snails | 0 | 43 +/- 22 | 0 | 0 | 0 | 0 |
| TOTAL INVERTS. | 6469 +/- 143 | 6319 +/- 1296 | 3236 | 4794 +/- 1419 | 4153 +/- 556 | 3010 +/- 447 |
| Mean no. of taxa / site. | 12.8 +/- 0.4 | 13.3 +/- 1.0 | 12 | 10.0 +/- 0.5 | 9.5 +/- 1.0 | 13.0 +/- 4.0 |

Figure 5b. The Classification of Sites by CLUSTAN using the Composition of Soil Invertebrate Groups

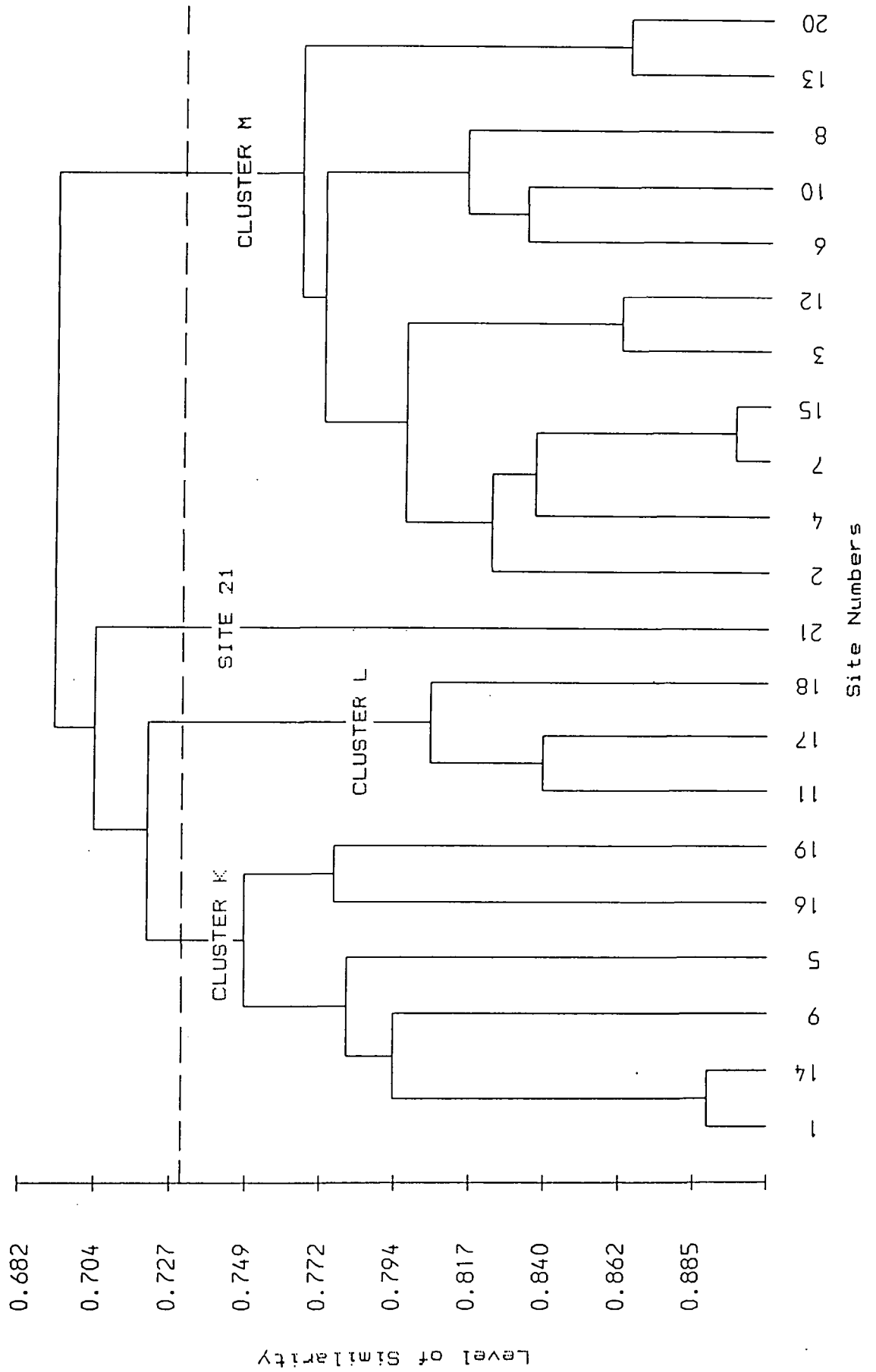


Table 5f. The pseudospecies abundance values for each indicator group of invertebrates extracted from turf samples at each of 21 sites in Kielder Forest. The sites are ordered according to Clustan classes. 1 (1 - 49 / 5m2), 2 (49 - 99 / 5m2), 3 (>100 / 5m2), 0 (not caught).

| Site Number | 1 | 14 | 9 | 5 | 16 | 19 | 11 | 17 | 18 | 21 | 2 | 4 | 7 | 15 | 3 | 12 | 6 | 10 | 8 | 13 | 20 |
|--------------------------|---|----|---|---|----|----|----|----|----|----|---|---|---|----|---|----|---|----|---|----|----|
| Chilopoda / Diplopoda | 0 | 0 | 1 | 0 | 2 | 1 | 3 | 3 | 3 | 0 | 0 | 1 | 0 | 0 | 2 | 3 | 1 | 2 | 0 | 0 | 0 |
| Caterpillars * | 0 | 0 | 1 | 1 | 1 | 1 | 2 | 2 | 0 | 2 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 |
| Carabidae | 3 | 3 | 1 | 2 | 2 | 3 | 2 | 1 | 2 | 0 | 0 | 2 | 1 | 2 | 1 | 1 | 0 | 0 | 0 | 1 | 1 |
| Hymenoptera | 3 | 2 | 2 | 3 | 1 | 3 | 3 | 3 | 0 | 3 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 |
| Coleoptera | 3 | 3 | 3 | 1 | 1 | 3 | 1 | 3 | 3 | 3 | 2 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 |
| Opiliones | 1 | 3 | 1 | 0 | 1 | 3 | 1 | 3 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 |
| "Slugs" | 1 | 2 | 2 | 1 | 0 | 3 | 2 | 3 | 2 | 1 | 0 | 0 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 |
| Isopoda | 0 | 0 | 1 | 0 | 0 | 0 | 2 | 3 | 3 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 |
| "Snails" | 0 | 0 | 0 | 0 | 1 | 0 | 2 | 3 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

* Caterpillars include both lepidoptera and sawfly larvae.

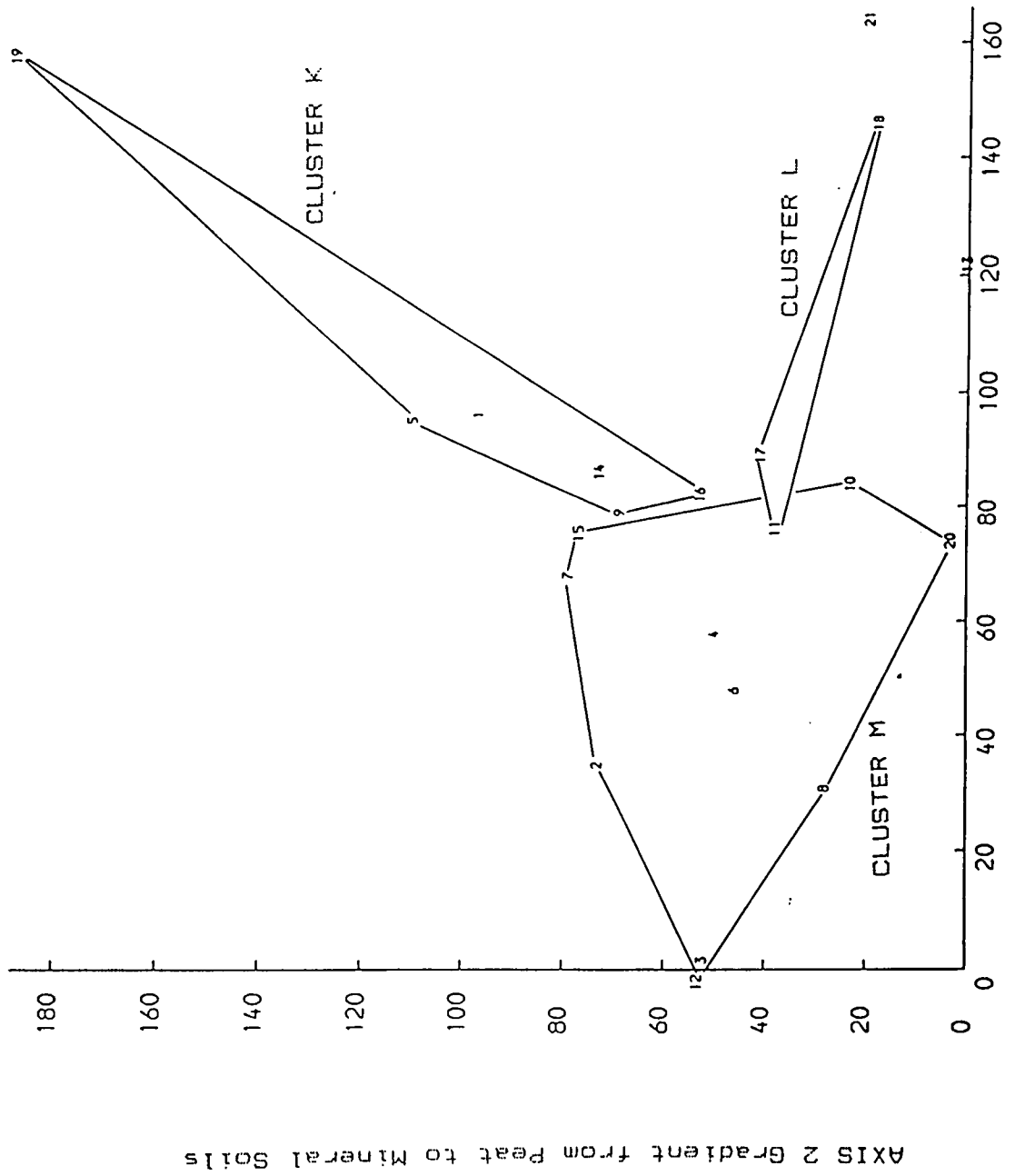
Hymenoptera and Coleoptera.

It appears that soil invertebrate cluster L is separated from cluster K largely because of the affinity to this cluster of the Isopoda and Mollusca (snails). These groups may require the mineral soils that are found in the sites within this cluster. They all belong to the carabid cluster B. Conversely, soil invertebrate cluster K, contains sites from both carabid clusters A and B which lie above peaty soils, whether deep peat or boulder clay derived stagnopodzols, peaty gleys or peaty skeletal soils. Isopoda and Mollusca (snails) are largely lacking from this group of sites. In this classification, as opposed to the carabid classification, sites based on mineral soils are more exclusive than those based on deep peat soils.

Figures 5c and 5d show the results of the sample and taxa scores from DECORANA. These agree with the CLUSTAN classification. Axis 1 of the taxa scores shows a gradient of decreasing tolerance to forestry. Those groups that are adversely affected by afforestation, eg. carabids, Hymenoptera, Coleoptera, slugs and Opiliones occur on the right hand side of the axis, whereas those that appear unaffected by afforestation, eg. Araneae, coleopteran larvae and dipteran larvae are found on the left hand side of the axis. Axis 1 of the sample scores places the forested sites of cluster M to the right of the non-forested sites.

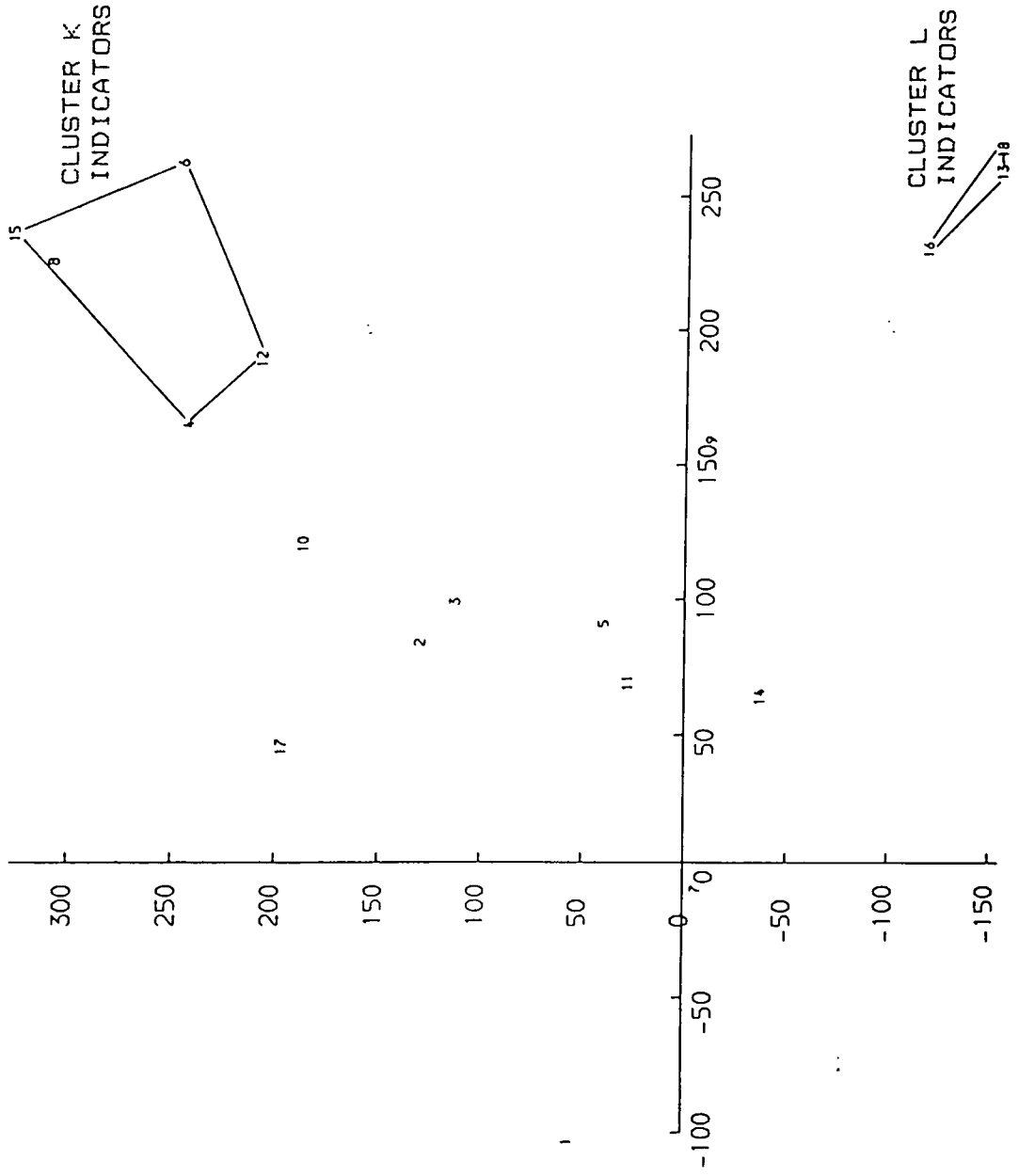
The second axes of figures 5c and 5d show a gradient from peat to mineral soils. In the taxa scores the groups which indicate mineral soils, Isopoda and Mollusca (snails), are separated from groups which are more generally distributed around the sites on all soil types. This is reflected in axis 2 of the sample scores so that the sites with the mineral soils of cluster L lie at the lower score end of the axis and those with peat soils tend towards the upper end of the axis.

Figure 5c. Plot of Site Scores Axis 1 and 2 Identified by DECORANA for Soil Invertebrate Groups



AXIS 1 Increasing Association with Forestry Practices

Figure 5d. Plot of Taxa Scores Axis 1 and 2 Identified by DECORANA for Soil Invertebrate Groups



AXIS 2 Gradient from Mineral Soils to Peat

AXIS 1 Decreasing Association with Forestry Practices

The classification of soil invertebrate group data differs from the carabid classification, especially with respect to the separation of the mineral soil sites from other non-forested sites, as opposed to the deep peat sites separated in the carabid classification. Both the conditions stipulated to suggest carabids may be reliable indicators of soil invertebrates therefore remain unfulfilled.

CONCLUSION

It is concluded that although carabids caught by pitfall trap may be reliable indicators of other invertebrates captured in this way, they cannot be used to assess the nature of the soil invertebrate fauna. To assess entire invertebrate communities greater emphasis should be placed on more rigorous sampling of likely communities by a greater range of methods such as extraction from soil samples.

DISCUSSION

This discussion firstly reviews the suitability of the multivariate techniques used, for the classification requirements of this study. Next it considers the application of the results of the classification, assessing the effects of afforestation to the original open ground fauna. Finally the use of carabids as a key group in assessing other invertebrates is critically considered.

Communities of carabids were found using multivariate methods of classification, but there is dispute over which classification technique is most appropriate for these purposes. Some favour the use of divisive classification methods such as TWINSpan, whilst others prefer to use agglomerative methods such as CLUSTAN. In this study both methods have been applied to the Kielder dataset to determine which is most appropriate.

I decided that CLUSTAN was the most appropriate method as the associations produced showed significantly different community structure characteristics such as the number of species and the percentage of catch accounted for by the five most abundant species. By taking account of both the presence and absence of species to produce a dissimilarity matrix of the sites, and then clustering the least dissimilar sites, CLUSTAN is likely to produce clusters of structurally similar communities. Also CLUSTAN is likely to isolate sites that have unique communities, such as site 21 in Kielder, which includes a range of species not found elsewhere.

The identification of unclassifiable sites has been a major criticism of CLUSTAN. Wishart (1978) when classifying water beetles by this method found that 30% of his sites were unclassifiable and had to be considered as outliers. Nevertheless, in this

study, the identification of an outlier is considered to be appropriate. Site 21 may be exposing the basis of an additional community present in Kielder and there is no need to enforce a site into a class if it is intrinsically different. Furthermore, by separating this site CLUSTAN may have drawn attention to a habitat that is rare in the area.

In this study TWINSpan was found to be less appropriate than CLUSTAN, due to the method by which a classification is produced. Each division is based on the major gradient in the data determined by the ordination of the sites with respect to the associated carabid fauna. It would be hoped that these gradients respond to the change in insect communities but this is not necessarily so, therefore the end classes may not be composed of distinct communities which display specific community structure characteristics. This was found to be a problem in the classification of Kielder carabids. Furthermore, sites are unlikely to be isolated, especially if, as in the case of site 21, it responds in the same way to a gradient than other sites but is essentially different in its carabid community.

Nevertheless, TWINSpan is a useful and widely used method of classification. Its use with respect to the Kielder data has shown major similarities with CLUSTAN. In both methods the main division separated the forested from non-forested sites whilst soil types figured strongly in the secondary division of non-forested sites. TWINSpan produced an ordered two-way table correlating sites and species which made it easier to interpret than CLUSTAN. For large scale classifications such as that undertaken by Luff *et al.* (1989) TWINSpan could be the most appropriate method. Also, where the effects of known environmental gradients or changes are being investigated, such as the effects of pasture improvement and management on the carabid communities of upland Britain (Rushton *et al.* 1989), TWINSpan's use of gradients to classify the data, and its identification of indicator species responding to the classification,

makes it the most appropriate technique to use.

The ordination technique, DECORANA, graphically represented the major patterns of variability among the species and the sites and was a useful aid to the interpretation of the classifications, especially with respect to the second axis.

The gradient of the second axis is related to the separation of sites without a closed forest canopy and related to soil types. Its use as a method for delimiting associations of carabids, however, is limited, the results suggesting the existence of a continuum of variation for both major axes. Classification techniques are required to simplify this continuum.

The classification produced from CLUSTAN analysis was chosen as the basis for determining the associations of carabids within the Kielder survey. Two communities were found to exist in areas where the forest canopy remained unclosed. It is interesting to compare how well these communities relate to those found in similar environments by other studies. In the initial I.T.E. survey, Good (1988) found that the vegetation in non crop areas of Kielder (including roads, rides, riversides and unplanted areas) could be classified into 4 groups depending on the soil type particularly the presence or absence of peat and where present, its depth. In all, 347 sites were sampled by Good. In this study only 14 unforested sites were sampled but a similar classification showed the same influence to be operating on carabid communities. Cluster A related to Good's upland blanket mire vegetation formed on deep peat, therefore stressing the distinctiveness of this habitat in terms of plant and animal communities. As with the plant community, the carabid community was impoverished and less diverse than the shallow peat and mineral soil sites comprising cluster B. The other 3 groups delimited by Good could not be distinguished in the carabid classification, neither could it find the distinct "road verge", "river" e.t.c. communities designated by Good. The replication of sites was inadequate to

allow such detailed patterns.

Coulson and Butterfield (1985) indicate that distinct invertebrate communities are recognisable on areas of peat and mineral soil in upland northern England. They identified seven invertebrate communities, and found the presence and depth of peat to be the overriding factor influencing the community composition. In a further paper, Butterfield and Coulson (1983) concentrated specifically on the carabid beetles and found a similar distinction of communities. The community of carabids forming association C2 at Kielder largely relates to their "Association B" which appeared on all but the driest and shallowest peat sites. However, 2 species of their "Association B", *Loricera pilicornis* and *Agonum fuliginosum*, were part of the community indicating non deep peat areas of Kielder and were in fact uncommon on the deep peat sites. This may be due to local variations in the preferences of these species.

Another survey (Luff *et al.* 1989) used data collected by a number of different methods. It was a much wider study which attempted to incorporate all habitats in North East England. Using TWINSpan, they identified an upland fauna from both wet and dry areas. The wet sites tended to be on peat, whereas the dry sites tended to be on mineral, well drained soils. Their most important upland species in terms of frequency of occurrence in the sites used included all the Kielder indicator species except for *Amara lunicollis*. However, their distribution among peat and mineral sites does not agree with that found in Kielder. *Patrobus assimilis* appears in more of Luff's sites on mineral soils than peat, but in Kielder it was absent from all mineral soil sites. Similarly, some of the indicator species of the mineral or shallow peat sites of Kielder appeared to be more common on the wetter peat sites in the study of Luff *et al.* (1989) including *Pterostichus niger*, *Carabus problematicus*, *C.violaceus*, *Loricera pilicornis* and *Leistus rufescens*. The division of the upland

sites by these other authors does not fully correspond to the division of sites using the carabids in Kielder.

Despite the non-conformity of carabid species among these studies, there does seem to be a consensus that the influence of peat is of paramount importance in determining the carabid communities of upland sites in northern England. The presence of deep peat in Kielder produces a separate community from that found on shallower peat or mineral soil sites. It is likely that this was the principal factor determining the composition and structure of the carabid communities in Kielder prior to afforestation. This has subsequently been modified by the effects of afforestation.

The effects of afforestation on this open ground fauna have been considerable. Good (1988) stated that the ground beneath closed canopy Sitka Spruce is largely devoid of vegetation. Despite the traps being set close to the forest edge very few carabids were found there. Carabids were more numerous in the thinned Norway Spruce site and the larch site, though it is not clear whether this reflects the tree species, the lower altitude, the higher mineral contents of the soils or some other factor. However, even in these two sites, the diversity of the carabid fauna is low, with the 5 most numerous species accounting for 96% of total individuals in the larch site and 97% in the Norway Spruce site.

It is likely that many factors operate to produce such an impoverished carabid fauna within the closed canopy forest and may include, for instance, a lack of light or lack of food. It was shown, however, that the species which are missing tend to be those which prefer habitats with a high moisture content or overwinter as adults. The effect of drainage, relative scarcity of vegetation and a closed canopy may all contribute to reducing ground and soil moisture and may result in fewer moisture preferring species present in closed canopy forest. In addition, a lack of suitable

hibernation sites may preclude the adult overwintering species. Such a severe impoverishment of the carabid fauna so close to the edge of the plantations suggests that conservation measures within these blocks would have limited effect. Any open areas where the trees have fallen as a result of windthrow are likely to have a very local effect only in increasing the diversity of the carabid fauna. This may be further limited by the surrounding forest forming a potential barrier to species that may disperse into the open conditions created.

There are few comparative studies concentrating on the effects of afforestation on open ground faunas or floras with which to compare these results. Ratcliffe (1985) points out that recent interest gives more attention to the gains than the losses especially with respect to birds, e.g. Moss (1978). Young plantations may have beneficial effects to some wildlife due to an increase in woodland edge habitat and restriction of access to grazing animals allowing a luxuriant flora to develop. These beneficial effects, however, would be expected to diminish as the trees grow and their canopies close. Sykes *et al.* (1989) monitored the changes caused by afforestation of a sheepwalk in Cumbria and noted a progressive deterioration of habitat with the growth of the forest. A numbers of plant species were lost as well as birds that prefer open grasslands or scrub such as the Whinchat and Skylark. Young (1985) in reviewing the effects of forestry on Lepidoptera stressed the adverse effects caused by both reductions in undergrowth containing essential food plants and by the development of adverse microclimatic conditions. Carabids, it would seem, are as severely affected by such processes as Lepidoptera.

More attention has been devoted to the effects on wildlife caused by the replacement of natural ancient forests, such as the primeval taiga of Scandinavia, by managed forests. This is generally considered to be detrimental due to the process of silvification whereby the natural undergrowth is modified (e.g. Marcstrom 1985).

However, according to Niemela *et al.* (1988), the carabid fauna was not found to be badly affected, the original fauna being already adapted to forest conditions. This is not the case in Kielder where a carabid fauna adapted to open conditions has been severely depleted.

The severe depauperisation of flora and fauna under closed canopy forest conditions leads to the conclusion that it is the areas between the forest blocks which are more important for conservation. These areas consist of both linear habitats and open spaces which are commonly thought of as providing important dispersal corridors and islands of favourable habitat for wildlife in a generally hostile environment. They can be managed for this end, but only under the limitations imposed by the original communities and it is not always clear what constitutes a favourable habitat. Criteria for conservation include typicalness and rarity. The typical habitats of the carabids of Kielder are the deep peat and non-deep peat uplands and examples of these habitats are likely to remain unforested. The disturbance of open areas by the planting of deciduous woodland or proximity of the forest blocks appears only to have a secondary effect on the original communities which are clustered primarily according to soil type. Active management is therefore not necessary to these typical habitats, they only require an undertaking to ensure they are adequately preserved in Kielder. Conversely, the preservation of rare habitats such as site 21 may require active management. In this case, the unique fauna identified would seem to be the result of the coincidence of a heavily grazed pasture and a stream. The high diversity of carabids found at this site may be dependent on the continuation of sheep farming. Unfortunately, in recent years the lettings in the Kielder area have been reduced.

Apart from these continuously open areas, other open areas will be temporarily and periodically restored around the forest as areas are clearfelled and replanted. It is

widely assumed that these areas will not regain their original flora and fauna before closed canopy conditions are once again enforced. Bibby (1986) found that there was no reversal to the original bird community prevailing before afforestation; instead there was a community containing some of the original species and some forest edge species. Ratcliffe (1985) stressed the different plant assemblages within these restock areas, with higher proportions of species typical of disturbed ground such as *Digitalis purpurea* and *Chamaenerion angustifolium*. However, I failed to find any major differences in the nature of carabid species within these temporary sites. Not only were they classified along with similar sites that had remained unforested indicating they possess a similar carabid community, but the prediction that a more opportunist and less moist preferring carabid fauna would be apparent was not substantiated. In fact the original carabid community would appear to quickly return to forested areas in the event of clearfelling indicating that the impoverishment of the carabid fauna during the forest rotation is only transient.

Although this survey is limited in extent and more studies are required to substantiate the findings, it would seem that only areas with a rare carabid community need to be protected during afforestation, otherwise, the carabid communities will persist by taking refuge within the temporary and permanent open spaces between the forest blocks until the canopy is felled.

Now that the carabid communities have been assessed and the impact of forestry practices described, it remains to be seen whether carabids are useful indicators of the invertebrate communities in general.

There was a good relationship between the numbers of carabids and the numbers of most other invertebrate groups caught by pitfall trap in both the identified clusters and individual sites of Kielder. Those that produced large numbers of carabids tended to

also produce large numbers of other invertebrates. Although this would appear to suggest that carabids are good indicators of other invertebrates, this cannot be confirmed without identification of at least one other taxonomic group to species to compare the distribution of the communities.

There was not a good relationship between the abundance of carabids and the groups sampled by soil extraction methods. Although closed canopy tree cover had an adverse effect on the abundance of soil invertebrates, the severe effect found with respect to the carabids was not evident, with overall densities remaining quite high and coleopteran larvae even increasing. The latter appears anomalous especially considering numbers of adult Coleoptera are much lower. Certain species of coleopteran larvae which thrive in closed canopy forest may reach high densities due to a lack of predators, but without speciation this cannot be investigated.

The classification by soil invertebrates of sites in open areas was very different to that of the carabids. Clusters A and B were not separated. Instead, the incidence of species that prefer mineral soils such as woodlice and snails, ensured that the mineral sites, rather than the deep peat sites, were isolated from other open sites. Site 21 was again separated, but through a low density of soil invertebrates.

The classification of sites by soil invertebrates appears to be different to that by the carabids. A number of explanations for this can be put forward;

- 1) Soil invertebrates are limited by different associations of factors than are carabids. Fly larvae, for instance, appear sensitive to the height and density of the ground vegetation rather than to the effects of a closed canopy of forest and type of soil.

2) Soil invertebrates were only sampled twice in the year in April and September, whereas the carabids were sampled continuously from April to September.

3) Soil sampling and pitfall trapping have different biases and consequently are likely to give different results. Catches in pitfall traps reflect activity and not density and some of the more sedentary soil animals, which appear to react to different environmental factors, may be grossly underestimated.

4) As with pitfall trapped invertebrate groups, different communities containing specific species of invertebrates may exist and conform with carabid communities. However, the use of densities of whole taxonomic groups rather than individual species precludes this analysis.

In summary, it can be concluded that the carabids may well be useful indicators of other mobile invertebrates that can be caught by pitfall traps. Identification to species of at least one other major group is needed to confirm this. The nature of the soil invertebrate communities cannot be assessed from the analysis of the carabid data. Other surveys should include further detailed sampling of soil invertebrates to give a more complete picture.

SUMMARY OF CONCLUSIONS

CLUSTAN was found to be the classification technique most appropriate to this study because it enabled the identification of associations of carabids which are distinct entities with respect to community structure. In open areas of Kielder Forest, these communities vary in response to the presence or absence of deep peat. The overriding environmental factor affecting the carabid communities, however, is the presence or absence of a closed forest canopy. Afforestation reduced the numbers of species with respect to the surrounding sites and excluded those of "moist" habitats and those that overwinter as adults. With removal of the forest canopy, however, the original community of carabids quickly reappears.

Carabids captured by pitfall traps may be reliable indicators of other ground dwelling invertebrates but they cannot be used as indicators of soil invertebrate communities. To assess entire invertebrate communities, therefore, it is vital to include other methods of sampling.

This study provides a preliminary assessment of upland plantation forest as a habitat for ground beetles. It has been shown that a conifer tree cover has drastic effects on the communities of these beetles but this is shortlived and the effects are reversed with removal of the cover. Further research is needed to substantiate and further the findings of this preliminary study.

APPENDICES

Appendix 1 Numbers of carabids caught

Appendix 2 Numbers of invertebrates caught

Appendix 3 Densities of soil invertebrates

Appendix 4 Correlation methods

APPENDIX 1

Table XX Numbers of Carabidae caught in the sites of Kielder 1988

| SITE NUMBER | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 |
|--------------------------------|----|----|----|----|----|---|----|---|-----|----|----|----|-----|----|----|----|----|----|-----|----|-----|
| <i>Cychus caraboides</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Carabus glabratus</i> | 3 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 7 | 0 | 0 | 6 | 1 | 0 | 0 | 0 | 0 |
| <i>C. granulatus</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>C. nemoralis</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 |
| <i>C. problematicus</i> | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 30 | 5 | 9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 |
| <i>C. violaceus</i> | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 4 | 6 | 1 | 28 | 2 | 8 | 29 | 70 | 9 |
| <i>Leistus rufescens</i> | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 9 | 0 | 3 | 1 | 0 | 6 | 2 | 5 | 9 | 19 | 19 | 15 | 0 |
| <i>Nebria brevicollis</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 0 | 85 | 0 | 206 |
| <i>N. gyllenhalii</i> | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 2 |
| <i>N. salina</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 155 | 0 | 0 |
| <i>Notophilus aquaticus</i> | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 6 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| <i>N. biguttatus</i> | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 5 | 2 | 1 | 1 | 12 | 0 | 0 | 2 | 0 | 2 | 37 | 5 | 1 |
| <i>N. germinyi</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>N. palustris</i> | 0 | 0 | 0 | 0 | 5 | 0 | 1 | 0 | 0 | 0 | 11 | 0 | 0 | 0 | 0 | 1 | 8 | 0 | 0 | 0 | 0 |
| <i>Elephrus cupreus</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| <i>Loricera pilicornis</i> | 1 | 0 | 0 | 0 | 0 | 0 | 21 | 0 | 2 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 11 | 0 | 24 |
| <i>Dyschirius globosus</i> | 1 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 3 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| <i>Clivina fossor</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 7 |
| <i>Patrobus assimilis</i> | 14 | 11 | 6 | 4 | 18 | 3 | 0 | 2 | 1 | 1 | 1 | 2 | 7 | 17 | 3 | 1 | 0 | 0 | 0 | 0 | 0 |
| <i>P. atrorufus</i> | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 119 | 0 | 0 |
| <i>Trechus obtusus</i> | 0 | 0 | 17 | 15 | 0 | 0 | 3 | 5 | 0 | 0 | 1 | 1 | 3 | 0 | 0 | 0 | 4 | 6 | 8 | 33 | 2 |
| <i>T. rubens</i> | 0 | 0 | 0 | 3 | 0 | 0 | 1 | 0 | 18 | 5 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 1 |
| <i>T. secalis</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 242 | 87 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Bembidion bruxellense</i> | 0 | 0 | 0 | 0 | 0 | 0 | 9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 1 |
| <i>B. unicolor</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| <i>Pterostichus adstrictus</i> | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 3 | 4 | 0 | 1 | 1 | 2 | 110 | 3 | 0 |
| <i>P. cristatus</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 7 | 0 | 0 | 0 |
| <i>P. diligens</i> | 29 | 0 | 5 | 0 | 23 | 0 | 2 | 0 | 0 | 0 | 15 | 0 | 144 | 13 | 7 | 8 | 8 | 1 | 4 | 0 | 4 |

CONTINUED:

| | | | | | | | | | | | | | | | | | | | | | | |
|--------------------------------|----|----|----|----|----|---|----|---|-----|-----|-----|----|-----|-----|----|-----|-----|-----|-----|-----|-----|-----|
| <i>P. madidus</i> | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 2 | 13 | 0 | 6 | 0 | 3 | 23 | 10 | 20 | 87 | 147 | 8 |
| <i>P. melanarius</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 7 |
| <i>P. niger</i> | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 8 | 0 | 2 | 14 | 1 | 36 | 5 | 1 | 6 | 1 | 11 |
| <i>P. nigrita</i> | 7 | 0 | 0 | 0 | 2 | 0 | 5 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 34 | 6 | 1 | 5 | 3 | 7 | 0 | 161 |
| <i>P. strenuus</i> | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 30 | 1 | 1 | 0 | 12 |
| <i>P. vernalis</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 14 |
| <i>P. versicolor</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 14 |
| <i>Abax parallelolopipedus</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 14 |
| <i>Calathus micropterus</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 6 | 0 | 0 | 0 | 30 | 0 | 5 | 0 |
| <i>Agonum albipes</i> | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 12 | 1 | 0 | 5 | 353 | 0 |
| <i>A. fuliginosum</i> | 0 | 0 | 0 | 0 | 10 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>A. muelleri</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 20 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 |
| <i>A. versutum</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 104 |
| <i>Amara aulica</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| <i>A. communis</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>A. lunicollis</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 18 | 0 | 2 | 3 | 0 | 0 | 0 | 0 | 0 | 1 | 2 |
| <i>Trichocellus placidus</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 52 | 0 | 1 | 2 | 0 | 2 | 0 | 0 |
| <i>Bradycellus harpalinus</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| TOTAL Numbers | 57 | 12 | 34 | 25 | 64 | 4 | 52 | 9 | 310 | 106 | 122 | 6 | 194 | 170 | 25 | 193 | 121 | 222 | 590 | 537 | 600 | |
| SPECIES Numbers | 8 | 2 | 7 | 5 | 8 | 2 | 15 | 3 | 10 | 8 | 19 | 5 | 18 | 14 | 8 | 18 | 23 | 16 | 17 | 12 | 24 | |

APPENDIX 2

Table XX Numbers of invertebrates caught by pitfall trap in the sites of Kielder 1988*

| SITE NUMBER | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 |
|----------------------|------|-----|-----|------|------|-----|------|-----|------|------|------|------|------|------|------|------|------|------|------|------|------|
| Nematocera | 76 | 30 | 125 | 408 | 133 | 58 | 76 | 178 | 882 | 455 | 728 | 607 | 118 | 242 | 301 | 1548 | 145 | 330 | 225 | 122 | 51 |
| Tipulidae | 47 | 28 | 49 | 30 | 16 | 41 | 5 | 17 | 43 | 39 | 5 | 19 | 9 | 30 | 89 | 124 | 129 | 132 | 1 | 31 | 6 |
| Diptera | 88 | 43 | 78 | 88 | 89 | 34 | 33 | 44 | 552 | 228 | 150 | 128 | 96 | 111 | 57 | 274 | 261 | 428 | 162 | 381 | 199 |
| Diptera larvae | 9 | 16 | 19 | 3 | 11 | 11 | 16 | 18 | 5 | 9 | 44 | 10 | 5 | 7 | 6 | 42 | 49 | 28 | 12 | 25 | 18 |
| Staphylinidae | 106 | 77 | 65 | 120 | 142 | 86 | 64 | 104 | 706 | 340 | 177 | 160 | 61 | 186 | 119 | 374 | 565 | 371 | 150 | 169 | 178 |
| Other Coleoptera | 60 | 46 | 35 | 77 | 45 | 27 | 98 | 26 | 537 | 235 | 103 | 110 | 26 | 67 | 38 | 173 | 390 | 250 | 185 | 495 | 206 |
| Coleoptera larvae | 9 | 22 | 9 | 9 | 99 | 7 | 7 | 13 | 45 | 94 | 107 | 23 | 11 | 44 | 76 | 34 | 156 | 94 | 60 | 78 | 82 |
| Hymenoptera | 240 | 47 | 90 | 9 | 1268 | 7 | 212 | 116 | 321 | 35 | 1078 | 17 | 282 | 125 | 275 | 412 | 180 | 56 | 20 | 34 | 277 |
| Lepidoptera larvae | 5 | 1 | 4 | 2 | 9 | 4 | 3 | 2 | 15 | 8 | 32 | 1 | 5 | 21 | 21 | 41 | 105 | 5 | 2 | 4 | 1 |
| Hemiptera | 139 | 38 | 29 | 62 | 46 | 21 | 24 | 18 | 59 | 19 | 141 | 24 | 50 | 55 | 74 | 319 | 287 | 69 | 25 | 44 | 85 |
| Araneae | 228 | 166 | 125 | 101 | 238 | 127 | 408 | 244 | 682 | 456 | 611 | 183 | 275 | 386 | 251 | 542 | 782 | 572 | 673 | 348 | 816 |
| Opiliones | 15 | 15 | 13 | 35 | 1 | 5 | 15 | 8 | 95 | 54 | 26 | 45 | 8 | 79 | 36 | 377 | 287 | 385 | 234 | 140 | 9 |
| Isopoda | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 10 | 16 | 3 | 1 | 1 | 1 | 0 | 1 | 79 | 59 | 10 | 0 | 2 |
| Chilopoda/ Diplopoda | 2 | 0 | 4 | 30 | 4 | 4 | 5 | 1 | 65 | 24 | 26 | 26 | 0 | 11 | 13 | 12 | 148 | 270 | 18 | 7 | 3 |
| Slugs | 46 | 2 | 6 | 1 | 3 | 0 | 6 | 2 | 9 | 2 | 66 | 3 | 1 | 17 | 41 | 6 | 126 | 46 | 16 | 1 | 27 |
| Worms | 15 | 0 | 0 | 4 | 1 | 2 | 0 | 0 | 12 | 8 | 6 | 1 | 1 | 26 | 1 | 6 | 55 | 21 | 36 | 23 | 34 |
| TOTAL | 1137 | 574 | 692 | 1007 | 2159 | 341 | 1033 | 802 | 4353 | 2132 | 3673 | 1371 | 1166 | 1620 | 1438 | 4438 | 3875 | 3355 | 2501 | 2562 | 2615 |

* Carabidae not included

APPENDIX 3

Table XX Densities of invertebrates per 5m² in the sites of Kielder 1988*

| SITE NUMBER | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 |
|-----------------------|------|------|-------|------|------|------|------|------|------|------|------|------|------|-------|------|------|-------|------|------|------|------|
| Nematocera | 270 | 815 | 3671 | 638 | 99 | 392 | 224 | 138 | 171 | 107 | 681 | 2971 | 25 | 1232 | 184 | 292 | 1821 | 38 | 127 | 216 | 92 |
| Other Diptera | 0 | 0 | 33 | 0 | 23 | 117 | 31 | 17 | 28 | 0 | 14 | 46 | 0 | 0 | 16 | 46 | 66 | 41 | 22 | 0 | 36 |
| Diptera larvae | 4008 | 1169 | 2738 | 1528 | 3063 | 1307 | 2320 | 742 | 1011 | 728 | 1353 | 2000 | 395 | 4566 | 1690 | 679 | 3817 | 3165 | 674 | 717 | 1145 |
| Carabidae | 109 | 0 | 30 | 74 | 96 | 0 | 39 | 0 | 32 | 0 | 69 | 17 | 22 | 239 | 55 | 99 | 39 | 79 | 128 | 15 | 0 |
| Staphylinidae | 651 | 157 | 761 | 315 | 403 | 246 | 353 | 303 | 776 | 401 | 838 | 349 | 133 | 1071 | 622 | 1572 | 1634 | 545 | 120 | 396 | 172 |
| Other Coleoptera | 106 | 50 | 16 | 32 | 16 | 0 | 34 | 17 | 108 | 30 | 32 | 0 | 43 | 148 | 17 | 48 | 448 | 138 | 406 | 24 | 261 |
| Coleoptera larvae | 680 | 379 | 2549 | 996 | 533 | 1204 | 1030 | 1981 | 734 | 614 | 1249 | 1651 | 495 | 967 | 536 | 898 | 2154 | 325 | 17 | 1712 | 113 |
| Hymenoptera | 321 | 48 | 14 | 0 | 240 | 16 | 36 | 0 | 60 | 0 | 186 | 0 | 33 | 91 | 17 | 46 | 156 | 0 | 364 | 0 | 119 |
| Lepidoptera larvae | 0 | 0 | 37 | 0 | 17 | 0 | 41 | 0 | 15 | 0 | 65 | 0 | 18 | 0 | 0 | 14 | 70 | 0 | 15 | 45 | 61 |
| Hemiptera | 223 | 0 | 19 | 89 | 450 | 0 | 115 | 0 | 29 | 0 | 38 | 15 | 0 | 166 | 89 | 375 | 261 | 0 | 13 | 0 | 0 |
| Araneae | 151 | 256 | 215 | 640 | 158 | 329 | 146 | 367 | 285 | 215 | 214 | 156 | 116 | 362 | 245 | 981 | 472 | 442 | 30 | 93 | 36 |
| Opliones | 24 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 31 | 0 | 32 | 0 | 30 | 368 | 30 | 205 | 228 | 77 | 134 | 39 | 0 |
| Isoptera | 0 | 0 | 0 | 0 | 0 | 20 | 0 | 0 | 46 | 20 | 62 | 0 | 0 | 0 | 0 | 0 | 598 | 568 | 0 | 0 | 19 |
| Chilopoda / Diplopoda | 0 | 0 | 71 | 18 | 0 | 37 | 0 | 0 | 14 | 61 | 347 | 241 | 0 | 0 | 0 | 78 | 373 | 156 | 32 | 0 | 0 |
| *Slugs* | 15 | 0 | 0 | 0 | 38 | 0 | 16 | 0 | 72 | 0 | 57 | 53 | 0 | 57 | 0 | 0 | 142 | 77 | 0 | 0 | 18 |
| *Worms* | 236 | 54 | 127 | 343 | 0 | 134 | 19 | 32 | 30 | 387 | 653 | 95 | 694 | 1035 | 69 | 349 | 1665 | 1906 | 215 | 902 | 1464 |
| P. Scorpions | 0 | 60 | 16 | 37 | 0 | 0 | 94 | 0 | 16 | 0 | 15 | 0 | 0 | 20 | 82 | 61 | 0 | 15 | 13 | 30 | 0 |
| Snails | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 57 | 0 | 0 | 0 | 0 | 16 | 124 | 190 | 0 | 0 | 0 |
| TOTAL | 6792 | 2988 | 10297 | 4710 | 5136 | 3802 | 4498 | 3597 | 3458 | 2563 | 5962 | 7594 | 2004 | 10322 | 3652 | 5759 | 14068 | 7762 | 2310 | 4189 | 3536 |

APPENDIX 4

The correlation of height/density of ground vegetation was undertaken using a Pearson product moment coefficient.

The independent axis: ground vegetation height/density was calculated by subjectively assigning "scores" to represent these site features.

VEGETATION HEIGHT

- vegetation 0-0.3m tall =1
- " " 0.3-1.0m tall =2
- " " greater than 1.0M =3

VEGETATION DENSITY

- vegetation covering 0-25% =1
- " " " " 25-75% =2
- " " " " 75-100% =3

The scores for height and density were multiplied together to give one value for each site. This was then correlated with the density of fly larvae in the soil calculated for each site.

REFERENCES

- Baars, M.A. (1979) Catches in pitfall traps in relation to mean densities of carabid beetles. *Oecologia* 41, 25-46.
- Bibby, C. (1986) Birds of restocked conifer plantations in Wales. *Journal of Applied Ecology*.
- den Boer, P.J. (1977) *Dispersal power and survival. Carabids in a cultivated countryside*. Miscellaneous paper Landbouwh Wageningen 14, 11-190.
- Butterfield, J. and Coulson, J.C. (1983) The carabid communities on peat and upland grasslands in northern England. *Holarctic Ecology* 6, 163-174.
- Cory, J.S. (1984) *Aspects of the ecology of predatory ground beetles as related to their pest control potential*. Unpublished Ph.D. thesis, University of Oxford.
- Coulson, J.C. and Butterfield, J. (1985) The invertebrate communities of peat and upland grasslands in the north of England and some conservation implications. *Biological Conservation* 34, 197-225.
- Forestry Commission (1984) *Census of Woodland and Trees*. Edinburgh.
- Greenslade, P.J.M. (1961) *Studies on the ecology of Carabidae (Coleoptera)*. Unpublished Ph.D. thesis, Department of Zoology, University of London
- Good, J.E.G., Williams, T.G. and Thomson, A.G. (1988) *Nature conservation in upland*

conifer forests. Unpublished progress report. Institute of Terrestrial Ecology, Bangor.

Halsall, N.B. and Wratten, S.D. (1988) The efficiency of pitfall trapping for polyphagous predatory Carabidae. *Ecological Entomology* 13, 293-299.

Hengeveld, R. and Hogeweg, P. (1979) Cluster analysis of the distribution patterns of Dutch carabid species. In: Orloci, L., Rao, C.R. and Stiteler, W.M. (Eds.) *Multivariate Methods in Ecological Work*. Maryland.

Hill, M.O. (1979) *DECORANA: A Fortran program for detrended correspondence analysis and reciprocal averaging*. Cornell University, New York.

Hill, M.O., Bunce, R.G.H. and Shaw, M.W. (1975) Indicator species analysis, a divisive polythetic method of classification, and its application to a survey of native pinewoods in Scotland. *Journal of Ecology* 63, 597-614.

Kloet, G.S. and Hinks, W.D. (1977) A check list of British insects. Part 3 Coleoptera and Strepsiptera. *Handbooks for the Identification of British Insects*. 4/3 Royal Entomological Society, London.

Lindroth, C.(1974) Coleoptera, Carabidae *Handbooks for the Identification of British Insects*. 4/2. Royal Entomological Society, London.

Lindroth, C. (1985, 1986) The Carabidae of Fennoscandia and Denmark. *Fauna Entomologica Scandinavica* 15, part 1 and 2.

Luff, M.L., Eyre, M.D. and Rushton S.P. (1989) Classification and ordination of

habitats of ground beetles (Coleoptera, Carabidae) in north-east England. *Journal of Biogeography* 16, 121-130.

Luff, M.L. and Rushton, S.P. (1989) The ground beetle and spider fauna of managed and unimproved upland pasture. *Agriculture, Ecosystems and Environment* 25, 195-205.

Marcstrom, V. (1985) Managing forests for wildlife in Sweden. In: Jenkins, D.J. (Ed.) *Trees and Wildlife in the Scottish Uplands*. I.T.E. Symposium no.17. Banchory.

Moss, D. (1978) Song bird populations in forestry plantations. *Quarterly Journal of Forestry* 72, 5-14.

Murdoch, W. (1967) Life history patterns of some British Carabidae (Coleoptera) and their ecological significance. *Oikos* 18, 25-32.

Niemela, J., Haila, Y., Halme, E., Lahti, T., Pajunen, T. and Puntila, P. (1988) The distribution of carabid beetles in fragments of old coniferous taiga and adjacent managed forest. *Annales Zoologici Fennici* 25, 107-119.

Ratcliffe, D.A. (1985) The effects of afforestation on the wildlife of open habitats. In: Jenkins, D.J. (Ed.) *Trees and Wildlife in the Scottish Uplands*. I.T.E. Symposium no.17. Banchory.

Rowan, A.A. (1985) The nature of British upland forests in the 1980s. In: Jenkins, D.J. (Ed.) *Trees and Wildlife in the Scottish Uplands*. I.T.E. Symposium no.17. Banchory.

Rushton, S.P., Luff, M.L. and Eyre, M.D. (1989) Effects of pasture improvement and



management on the ground beetle and spider communities of upland grasslands. *Journal of Applied Ecology* 26, 489–503

Sneath, P.H.A. and Sokal, R.R. (1973) *Numerical Taxonomy*. Freeman, San Francisco.

Southwood, T.R.E (1978) *Ecological Methods*, second Edition. Chapman and Hall, London.

Sykes, J.M., Lowe, V.P.W. and Briggs, D.R. (1989) Some effects of afforestation on the flora and fauna of an upland sheepwalk during 12 years after planting. *Journal of Applied Ecology* 26, 299–320.

Turin, H. and den Boer, P.J. (1988) Changes in the distribution of carabid beetles in the Netherlands since 1880. II. Isolation of habitats and long term trends in the occurrence of carabid species with different powers of dispersal (Coleoptera, Carabidae). *Biological Conservation* 44, 179–200.

Wishart, D. (1978) *CLUSTAN users manual*, third edition. University of Edinburgh.

Young, M.R. (1985) The effects of commercial forestry on woodland Lepidoptera. In: Jenkins, D.J. (Ed.) *Trees and Wildlife in the Scottish uplands*. I.T.E. Symposium no.17. Banchory.